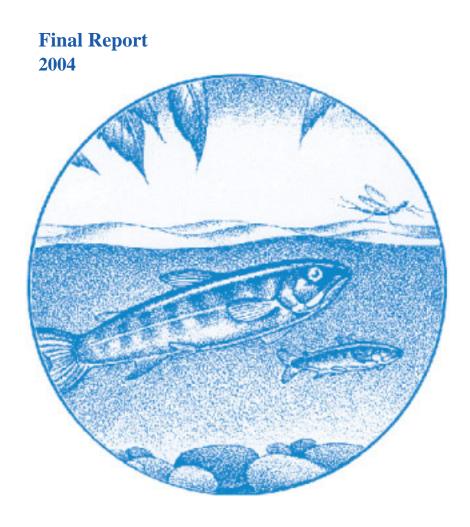
# **Assessment of Smolt Condition: Biological and Environmental Interactions**

### The Impact of Prey and Predators on Juvenile Salmonids





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## Assessment of Smolt Condition: Biological and Environmental Interactions

(BPA Project No. 1987-401-00)

#### **Final Report**

The impact of prey and predators on juvenile salmonids

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#### **Assessment of Smolt Condition: Biological and**

#### **Environmental Interactions**

#### **Executive Summary**

The Bonneville Power Administration (BPA) has funded the Assessment of Smolt Condition project since 1987. During that time the project changed frequently to meet the information needs of fish managers by conducting studies throughout the Columbia River basin. Past research has examined the influence of smolt physiological development and health on migration rate; differences in development and migration rates of smolts of hatchery or wild origins; and the impacts of hatchery practices on smolt development. The Smolt Assessment Project will not continue beyond 2004, and here we report on the final study of the project in which we used bioenergetics modeling to investigate predation on juvenile salmonids by northern pikeminnow, smallmouth bass, and walleye in the lower Columbia River reservoirs.

The first portion of the work reported here investigated the role of anadromous preyfish and water temperature in the growth and salmonid consumption of northern pikeminnow. This modeling will be combined with similar work completed as part of another BPA-funded project to identify large-scale northern pikeminnow predation patterns in the lower Snake and Columbia rivers. In attempting to understand the interactions driving smolt predation, our research identified three spatially separate northern pikeminnow predation patterns in the lower Columbia River basin. The biotic and abiotic factors contributing to these spatially distinct northern pikeminnow growth and predation patterns are: (1) release of large numbers of hatchery salmonids into the free-flowing Columbia River below Bonneville Dam, (2) rearing and emigration of large numbers of invasive American shad in the lower Columbia River reservoirs, and (3) low numbers of anadromous preyfish and warmer water temperatures in the lower Snake River reservoirs. Identification of these predation patterns provides management agencies with large-scale spatial information on the factors driving northern pikeminnow predation on juvenile salmonids in different areas of the lower Columbia River basin, and opportunities for development of innovative predation control measures.

The second portion of this study focused on the potential impact of larval and juvenile American shad, an invasive preyfish, on the growth and salmonid consumption of invasive predators in the lower Columbia River reservoirs. We estimated the late summer and fall diet of smallmouth bass and walleye, and used size-at-age data on smallmouth bass (Beamesderfer and Ward 1994) and walleye (Tinus and Beamesderfer 1994) collected in John Day Reservoir to run bioenergetics simulations under various prey and water temperature scenarios. Most significantly, our modeling on invasive aquatic predators suggests that a relatively small increase in the growth of smallmouth bass due to American shad preyfish in the late summer and fall diet could potentially result in a large increase in the proportion of juvenile salmonids consumed by this predator. Our results support earlier research and reinforces concern expressed by numerous authors that smallmouth bass predation may result in heavy losses of subyearling fall Chinook (Gray and Rondorf 1986; Curet 1993; Tabor et al. 1993; Poe et al. 1994; Zimmerman 1999; Duran et al. 2003; Petersen et al. 2003). Because of their smaller size and later migration period, wild fall Chinook from the Hanford Reach and Snake River may be more vulnerable to smallmouth bass predation than hatchery fish. Juvenile salmonids may also be vulnerable to smallmouth bass predation whenever foraging or flow patterns bring migrants near shorelines, or migrants are delayed in dam forebays, particularly later in the spring once water temperatures have warmed.

Bioenergetics modeling also suggests that the growth of walleye is enhanced by a late summer and fall diet of American shad. Unlike smallmouth bass, the increased walleye growth predicted with a fall diet that includes American shad produced only a modest rise in salmonid consumption. Bioenergetics simulations also suggest that warmer summer and fall water temperatures in the impounded lower Columbia River contribute substantially to the growth rates of smallmouth bass and walleye. The increased feeding rate of these introduced aquatic predators in response to warmer water temperatures during the summer months suggests these species may primarily impact subyearling fall chinook in the lower Columbia River.

#### Introduction

Emigrating juvenile salmon and steelhead face large numbers of aquatic predators as they move through the lower Snake and Columbia river migration corridors (Table 1 and 2). Three invasive species known to consume emigrating salmonids are smallmouth bass (Micropterus dolomieu), walleye (Stizostedion vitreum), and channel catfish (Ictalurus punctatus) (Gray and Rondorf 1986; Poe et al. 1991; Zimmerman 1999). The introductions of these predators into the Columbia River basin appear to be extremely successful; smallmouth bass and channel catfish are distributed in lower mainstem Columbia and Snake river reservoirs, smallmouth bass have also invaded free-flowing reaches, and walleye are established in the Columbia River reservoirs. Estimates of population densities, growth characteristics, and fecundity suggest that reservoir conditions in the lower Columbia River reservoirs are quite favorable for these introduced predators (Maule and Horton 1984, 1985; Poe et al. 1994; Zimmerman and Parker 1995).

Another invasive species, the anadromous American shad (<u>Alosa sapidissima</u>) may be a contributing factor in the success of these invasive predators. The American shad is native to the east coast of North American, and was introduced into the Sacramento River, California over a century ago (Petersen et al. 2003). Within a few years after the Sacramento River introduction, adult American shad spread north into other coastal tributaries and invaded the Columbia River (Petersen et al. 2003). Historically, the American shad population in the Columbia River was limited to the lowest portion of the river by the swift current and cascades of the Columbia River. Hydropower development of the lower Columbia River, beginning in 1938 with Bonneville Dam, continued to block upstream access to American shad until fish ladder modifications were completed in the 1970s (Petersen et al. 2003). These ladder modifications improved passage for adult salmonids, but also opened the impounded reservoirs of the lower Columbia River reservoirs to American shad invasion (Monk et al. 1989; Petersen et al. 2003). Large numbers of juvenile American shad now rear in and emigrate though the lower Columbia River and its reservoirs (Petersen et al. 2003). In recent years, the number of returning adult American shad has often outnumbered adult salmon and steelhead passing Bonneville Dam, and the largest American shad run ever recorded at Bonneville Dam was 4.7 million fish in 2003 (http://www.fpc.org).

The large number of juvenile American shad rearing and emigrating through the lower Columbia River reservoirs may be an important and largely unrecognized link to the predation mortality incurred by salmon and steelhead smolts. Juvenile American shad may influence the predator populations that prey on emigrating salmonids in several key ways. First, juvenile American shad are abundant in the reservoirs from mid-summer through fall, providing forage for predators at a time when juvenile salmonids are scarce. Second, juvenile American shad are also an energy-rich meal for predators, providing more calories/gram than most other prey available in the Columbia River. Third, because of hydroelectric impoundment, water temperatures in the lower Columbia River reservoirs remain warmer longer into the fall than under pre-impoundment conditions (Quinn and Adams 1996; Quinn et al. 1997; Sauter and Petersen, Report C in prep.). Warmer water temperatures increase the metabolic demand and fall foraging activities of aquatic piscivores. The combination of abundant juvenile American shad and warmer fall water temperatures provides aquatic predators with favorable fall growth conditions that did not exist 60 years ago.

Warmer fall water temperatures and abundant numbers of American shad in the lower Columbia River migration corridor may directly contribute to the population size, annual growth rate, and reproductive potential of aquatic predators preying on salmon and steelhead smolts. Predation research on juvenile salmonids has primarily targeted a native predator, the northern pikeminnow (<u>Ptychochelius oregonensis</u>) for study and management, while the predation impact of invasive piscivores on emigrating smolts has received less attention. Much is known about the seasonal diet (Poe et al. 1991; Zimmerman

1999; Sauter and Petersen Report B, in preparation), behavior (Poe et al. 1994), density (Beamesderfer et al. 1990; Beamesderfer and Rieman 1991; Parker et al. 1995), growth rate (Parker et al. 1995; Petersen Report A, in preparation), and fecundity (Knutsen and Ward 1997) of northern pikeminnow at various locations in the Columbia River basin.

Prior to the implementation of the northern pikeminnow management program, this native predator consumed an estimated 16.4 million juvenile salmonids annually in the impounded mainstem Snake and Columbia rivers (Beamesderfer et al. 1996). An estimated 1.4 million juvenile salmonids were consumed each year in John Day Reservoir alone (Petersen 1994). Based on northern pikeminnow population and diet estimates from 1983 - 1986, and prey digestion rates, 78% of the juvenile salmonid losses in John Day Reservoir are due to northern pikeminnow predation and the remaining 22% is attributed to smallmouth bass and walleye (Poe et al. 1991; Rieman et al. 1991; Vigg et al. 1991). Channel catfish are also a potentially important predator on juvenile salmonids in lower Snake and Columbia river reservoirs (Gray and Rondorf 1986; Zimmerman and Parker 1995) but were not included in salmonid loss estimates.

Recently, Sauter and Petersen (Report B, in preparation) used bioenergetics modeling to explain observed growth differences between northern pikeminnow collected from the free-flowing lower Columbia River compared to lower Snake River reservoirs. Bioenergetics simulations suggested that diet and annual temperature regime could explain the observed differences in predator growth between the two locations and a more complex pattern of northern pikeminnow predation dynamics in the Columbia River basin began to emerge (Sauter and Petersen, Reports B, C and D, in preparation). In the current paper, we expand on previous northern pikeminnow bioenergetics modeling to (1) model the influence of invasive American shad on northern pikeminnow growth and smolt consumption in the lower Columbia River reservoirs, (2) identify some of the spatial and temporal northern pikeminnow predation patterns in the lower Columbia River migration corridor, and (3) model the potential impact of invasive prey and predators on migrating juvenile salmonids.

#### **Methods**

#### Study Area

Previous bioenergetics modeling on northern pikeminnow sought to explain observed growth differences between populations in the lower Snake River reservoirs and the free-flowing Columbia River below Bonneville Dam (Petersen and Sauter, Report B in preparation). The current study examines the impact of invasive American shad on the growth and smolt consumption of northern pikeminnow and two invasive predators, smallmouth bass and walleye, in the lower Columbia River reservoirs (LCRR). Our study area extended from Bonneville Dam forebay to McNary Dam tailrace, and includes Bonneville, The Dalles, and John Day reservoirs.

#### **Data compilation**

We compiled data from a variety of published and unpublished sources to investigate hypotheses about predator growth and smolt consumption in the LCRR. No additional field effort was conducted to fulfill the data requirements.

Table 1. Common invasive aquatic predator and preyfish species found in the migration corridor of the lower Columbia River (Barfoot et al. 2002), their lifestage at that trophic level and migratory status.

				Migratory
Trophic Level	<b>Common Name</b>	Scientific Name	Life stage	status
<u>Predator</u>	Smallmouth bass	Micropterus	juveniles and	resident
		dolomieu	adults $> 75 \text{ mm}$	
	Walleye	Stizostedion vitreum	adult	resident
	Channel catfish	Ictalurus punctatus	adult	resident
Potential Preyfish	American shad	Alosa sapidissima	juvenile	anadromous
<u>110y11311</u>	Common carp	Cyprinus carpio	juvenile	resident
	Bluegill	Lepomis macrochirus	juvenile	resident
	Pumpkinseed	Lepomis gibbosus	juvenile	resident
	Crappie	Pomoxis spp.	juvenile	resident
	Yellow perch	Perca flavescens	juvenile	resident
	Bullhead	Ameiurus spp.	juvenile	resident

Table 2. Common native predator and preyfish species of the lower Columbia River, their lifestage at that trophic level and migratory status (Poe et al. 1991; Zimmerman 1999).

				Migratory
Trophic Level	<b>Common Name</b>	ne Scientific Name Life Stag		status
<u>Predator</u>	Northern	Ptychocheilus	Juveniles and	resident
	pikeminnow	oregonensis	adults >250 mm	
Potential preyfish	Chinook salmon	Oncorhynchus tshawytscha	parr and smolts	anadromous
	Steelhead	Oncorhynchus mykiss	parr and smolts	anadromous
	Peamouth	Mylocheilus caurinus	juveniles	resident
	Chiselmouth	Acrocheilus alutaceus	juveniles	resident
	Redside shiner	Richardsonius balteatus	juveniles/adults	resident
	Longnose dace	Rhinichtys cataractae	juveniles/adults	resident
	Largescale sucker	Catostomus macrocheilus	juveniles	resident
	Bridgelip sucker	Catostomus columbianus	juveniles	resident
	Sand roller	Percopsis transmontana	juveniles/adults	resident
	Sculpins	Cottus. spp.	juveniles/adults	resident
	Lamprey	Petromyzontidae spp.	juveniles	resident

#### **Bioenergetics modeling**

We used bioenergetics modeling to investigate the growth and smolt consumption of northern pikeminnow, smallmouth bass, and walleye under various diet and water temperature scenarios. Bioenergetics simulations were developed to test the hypothesis that the observed growth patterns of predators in the LCRR can be explained by the presence of American shad in predator diets and the annual water temperature regime of impoundments. The bioenergetics models were also used to estimate smolt consumption of predator populations in the LCRR under the current temperature regime and to predict smolt consumption by predators growing without juvenile American shad in their diets. Since changes in the availability of juvenile American shad in predator diets might also affect the overall availability of prey, we also predicted smolt consumption by predator populations growing without American shad in their diets and under reduced feeding opportunities. Although we consider channel catfish a potentially important predator on juvenile salmonids in LCRR, there were insufficient growth and diet data available on this species to develop simulations.

Bioenergetics modeling of northern pikeminnow, smallmouth bass, and walleye were run using the software of Hanson et al. (1997). For the northern pikeminnow simulations we used the physiological parameters developed by Petersen and Ward (1999). Physiological parameters for our smallmouth bass model were taken from Roell and Orth (1993), and walleye parameters were developed by Kitchell et al. (1977). Bioenergetics models are expanded versions of the general form of the bioenergetics balanced energy equation:

growth = consumption - (respiration + egestion + excretion).

See Hanson et al. (1997) or Petersen and Ward (1999) for full model development.

We compared the observed growth of each predator species under the current water temperature regime and diet that includes American shad (nominal bioenergetics model) with the predicted growth of predators under three scenarios: (1) current water temperature regime without American shad in predator diets, (2) historic water temperature regime with American shad in the diets, and (3) historic water temperatures without American shad in the diets. Estimates of current smolt consumption by each predator species were generated with the nominal bioenergetics models. Two models were run to predict smolt consumption by predator populations under "reduced growth" and "reduced growth and feeding" conditions. The "reduced growth" model predicted salmonid consumption by predators growing under a diet without juvenile American shad, while the "reduced growth and feeding" model predicted salmonid consumption by predator populations growing without juvenile American shad in their diet and under reduced feeding opportunities.

Input parameters for the bioenergetics models included the first and last day of the analysis, and the starting and final mass (g) or total consumption (p-value estimate) of predator cohorts. These input parameters are explained in more detail below.

#### *Seasonal growth of predators*

Our bioenergetics simulations allowed northern pikeminnow to grow from April 1 to November 30 (243 days), and smallmouth bass and walleye to grow from April 17 to November 30 (234 days) under the LCRR temperature regime. The growth period of predators was based on the 10-year average date that reservoir water temperatures dropped below  $10^{\circ}$  C in the fall (www.cqs.washington.edu/dart/dart.html). We assumed the growth of predators is very low or negative when water temperature is below  $10^{\circ}$  C ( $\pm$  0.5° C), but allowed the spring growth period of northern pikeminnow to begin 17 days earlier than that of invasive predators to coincide with the early spring

smolt migration (Petersen and Ward, 1999). We assumed the native northern pikeminnow is better adapted to begin feeding at slightly lower water temperatures in the spring than invasive predators in the LCRR. Optimal temperatures for growth are higher for adult walleye (20° - 28° C) and smallmouth bass (26° - 29°C) than for northern pikeminnow (20.1° - 22.7° C) (Armour 1993a and b; Petersen and Ward 1999).

We used northern pikeminnow size-at-age data from 1990 – 1992 to construct von Bertalanffy growth curves for fish collected from the LCRR (Petersen, Report A in preparation). These data were collected prior to the large-scale bounty removal of northern pikeminnow. Growth increments from the von Bertalanffy analyses were converted from fork length to mass (g) using the linear model developed by Parker et al. (1995). For the invasive predators, we used size-at-age data for smallmouth bass collected from the upper John Day Reservoir in 1982 – 1986 (Beamsderfer and Ward 1994) and walleye collected from John Day Reservoir fish in 1990 -1991 (Tinus and Beamsderfer 1994). Predator size-at-age data were used in the nominal bioenergetics models to estimate the feeding level (p-value) of predator cohorts.

#### Proportion of maximum consumption

The proportion of maximum consumption or "p-value" in the bioenergetics model represents an estimate of the average feeding rate for a cohort of fish during the simulation period. We fit a nominal p-value to each predator cohort by inputting the observed size-at-age data into the nominal bioenergetics model for each predator. Constant p-values for each predator species could not be used since p-values decline as fish increase in size.

We also generated reduced p-values with the nominal bioenergetics model to estimate smolt consumption under the reduced growth and feeding model. For northern pikeminnow and smallmouth bass, the observed final size of each predator cohort was input into the nominal bioenergetics model as the starting and final size to generate a reduced p-value. We fit a reduced p-value to the final size rather than the starting size of a cohort for northern pikeminnow and smallmouth bass because this approach resulted in lower p-values and estimates of smolt consumption in the reduced growth and feeding model than p-values fit to the starting size of the cohort. For walleye, it was necessary to generate a reduced p-value with the observed starting size of cohorts rather than the final size for modeling reduced growth and feeding conditions. Reduced p-values generated from the final size of walleye cohorts produced unrealistically high smolt consumption estimates under the reduced growth and feeding model; estimates exceeded those made with the nominal model. The percent change in smolt consumption between the nominal model and the reduced growth and reduced growth and feeding models were used to estimate the lower and upper bounds of smolt consumption by predator populations.

We found that the fitted p-values for predator cohorts did not decrease uniformly as fish increased in size. We conserved the proportional relationship between the observed size-at-age of cohorts and the feeding level necessary to achieve (or maintain) that size by fitting p-values to the observed size-at-age data for predator cohorts in the nominal bioenergetics model and using those p-values in the reduced growth and reduced growth and feeding models. In the case of the reduced growth model, we conserved the proportional relationship between the starting and final size of a cohort and the feeding level necessary to achieve that size. For the reduced growth and feeding models on northern pikeminnow and smallmouth bass, the proportional relationship between the final size of a cohort and the feeding level necessary to maintain that size was conserved from the nominal bioenergetics model. In the case of walleye, we maintained the proportional relationship between the starting size of a cohort and the feeding level from the nominal bioenergetics model.

#### Predator growth simulations

Using size-at-age growth increments and the corresponding nominal p-values, we interpolated p-values for five predator starting sizes (mass, g) (Table 3). The interpolated p-values were input into the bioenergetics model for each predator along with the starting size of cohorts to predict predator growth under the current water temperature regime without American shad preyfish (simulation A), and under the historic water temperature regime with (simulation B) and without (simulation C) American shad preyfish in predator diets (Table 4). The five starting sizes were chosen to predict growth across the size range of each predator population.

#### Smolt consumption simulations

Using the nominal bioenergetics model for each predator species, we estimated the current smolt consumption of predator populations in LCRR. We predicted smolt consumption of predators for the "reduced growth" and "reduced growth and feeding" models under current water temperature conditions and diets without American shad. Current smolt consumption by predator populations was determined by inputting the nominal p-values fit to the observed starting and final size of predator cohorts with the observed (northern pikeminnow) or extrapolated (smallmouth bass and walleye) seasonal diet of predators. For the "reduced growth" model, an estimate of smolt consumption by each predator cohort was made by inputting the predicted starting size of the predator cohort growing without American shad in their diet with the nominal p-value estimate for the cohort. Since the proportional relationship between cohort growth and feeding level observed in the nominal bioenergetics model is not constant, we maintained the same proportional relationship in the "reduced growth" model by using the nominal pvalues. The reduced growth model provides a lower bound to predator smolt consumption estimates for each predator without American shad in the diet. To model "reduced growth and feeding" conditions for northern pikeminnow and smallmouth bass, we used the predicted final size of a predator cohort growing under a diet without American shad as the starting size input with the reduced p-value for the cohort to generate an estimate of smolt consumption. This approach did not work for walleye because the predicted final size of cohorts generated unrealistically high estimates of smolt consumption since reduced p-values changed little between walleye cohorts older than 3 years. For walleye, we used the predicted starting size of each cohort input with reduced p-value for the starting size to generate an upper bound for smolt consumption.

To estimate the cumulative annual smolt consumption of each predator species growing under a diet with and without American shad, we used the observed size-at-age frequency data reported for northern pikeminnow (1990, Columbia River Reservoirs, female fish only (Parker et al. 1995)), walleye (1990 – 1991, John Day Reservoir, both sexes (Tinus and Beamsderfer 1994)), and smallmouth bass (1990 – 1992, lower Columbia River basin, both sexes (Zimmerman and Parker 1995)) to establish the age structure of a 1000 fish population. The number of individual predators in each age class of the 1000 fish population was then multiplied by the estimated annual smolt consumption of an individual predator of age x (years) and summed across all cohorts that were potential predators (> 250 mm FL for northern pikeminnow;  $\geq$  200 mm FL for walleye (Poe et al. 1991);  $\geq$  75 mm FL for smallmouth bass (Beamsderfer and Ward 1994)) to get the cumulative annual smolt consumption for each predator species growing under a diet with and without American shad.

Table 3. Starting weights (mass, g) of northern pikeminnow, smallmouth bass and walleye used in bioenergetics growth simulations.

Modeled starting mass (g) for predator growth							
Northern pikeminnow	Smallmouth bass	Walleye					
100	200	300					
400	600	1000					
750	1000	3000					
1100	1200	4000					
1400	1400	5000					

Table 4. Five starting sizes of northern pikeminnow, the predicted final mass (g) of fish, and the nominal p-values used to estimate final mass (g) under current water temperature and dietary conditions. Reduced p-values, used to estimate the smolt consumption of predators under reduced growth and feeding conditions, are given here for comparison purposes only, since smolt consumption estimates were calculated across all predator cohorts rather than the five starting sizes.

		Proportion of maximum consumption (p-value) used in					
Starting	Final	bioenergetics runs:					
mass	mass						
(g)	(g)	nominal	reduced				
100	219	0.313258	0.211887				
400	543	0.241311	0.191006				
750	876	0.211431	0.182709				
1100	1197	0.194791	0.178005				
1400	1466	0.184747	0.175179				

#### Diet of Northern pikeminnow

Detailed seasonal data on the diet of predators is needed for a complete bioenergetics modeling effort. Northern pikeminnow gut contents collected for previous diet studies in the LCRR by boat electroshocking provided data on the spring and summer diet (Poe et al. 1991; Shively et al. 1991; Petersen et al. 1993; Zimmerman 1999). Many of these studies tended to concentrate sampling effort in tailrace and forebay boat restricted zones (BRZ) near dams where northern pikeminnow congregate to prey on large numbers of juvenile salmonids. We incorporated data that was collected outside the BRZ of the dams into the generalized diet constructed for bioenergetics modeling. The fall diet of northern pikeminnow was constructed from fish caught by anglers and collected by the northern pikeminnow management program (NPMP). Angler-caught northern pikeminnow were primarily collected from midreservoir locations, and did not include any BRZ fish (Sauter and Petersen; Report B, in preparation). Based on these data, we constructed a generalized seasonal profile of the northern pikeminnow diet with and without juvenile American shad for the LCRR. The diet of northern pikeminnow was divided into five categories of prey: salmonids, American shad (AMS), other fish, crustaceans, and miscellaneous. We constructed the summer and fall diet so that American shad supplemented and then replaced the juvenile salmonid portion of the diet in August. The miscellaneous category consisted of prey with relatively low caloric value such as mollusks, insects, and plant material. Changes in the proportion of juvenile salmonids and American shad in the northern pikeminnow diet shifts the proportions of crustaceans and miscellaneous prey during some time periods since diet proportions must total 100% to run the bioenergetics model.

For the fall diet simulations without American shad, we assumed that northern pikeminnow would increase their predation slightly on "other fish" (+5%) if juvenile American shad were not available. The observed and hypothesized northern pikeminnow diets are summarized in Table 5.

Table 5. Observed and hypothetical northern pikeminnow diets for the LCRR used in bioenergetics modeling. The observed seasonal diet of northern pikeminnow consisted of 25% American shad (AMS); the effect of a hypothetical fall diet without American shad on northern pikeminnow growth was also modeled.

Time period	Prey category (%)							
_	salmonids	AMS	crustaceans	miscellaneous				
	Observ	ed seasonal d	liet of northern	n pikeminnow				
	wit	h 25% Amer	ican shad in th	e fall diet				
April/May	40	0	10	35	15			
June/July	10	0	10	40	40			
Aug 1 – 14	10	10	10	35	35			
Aug $15 - 31$	0	25	5	35	35			
Sept/Oct	0	25	5	35	35			
Nov/Dec	0	10	10	40	40			
	Hypothet	cical seasonal	diet of northe	rn pikeminnow	V			
		without	American sha	d				
April/May	40	0	10	35	15			
June/July	10	0	10	40	40			
Aug 1 – 14	10	0	10	40	40			
Aug 15 – 31	0	0	10	45	45			
Sept/Oct	0	0	10 45		45			
Nov/Dec	0	0	10	45	45			
Proportion								
indigestible <sup>a</sup> :	0.033	0.0165	0.0165	0.1	0.4			

<sup>&</sup>lt;sup>a</sup> Stewart et al. (1983) and Petersen and Ward (1999)

Sources: Petersen et al. 1990, 1992, & 2000; Poe et al. 1991; Shively et al. 1991; Zimmerman 1999; Sauter and Petersen Report B, in preparation.

#### Diet of Invasive predators

We based the fall diet of smallmouth bass and walleye on previous spring and summer diet studies on these species (*see* Poe et al. 1991; Shively et al. 1991; Zimmerman 1999). Juvenile salmonids are available to smallmouth bass and walleye from early April through much of August in LCRR. Crayfish are an important component of the smallmouth bass diet, while walleye feed almost entirely on preyfish (Poe et al. 1991; Shively et al. 1991; Zimmerman 1999). For our bioenergetics simulations, we assumed that the fall diet of these invasive predators was an extension of their spring and summer diets, and that juvenile American shad became important in the diet of these predators in early August. We constructed the late summer and fall diet of smallmouth bass (Table 6) so that the portion of juvenile salmonids in the diet was supplemented and then replaced by juvenile American shad. Changes in the proportion of juvenile salmonids, American shad, and other preyfish in predators' diets shifts the proportions of crustaceans and miscellaneous prey during some time periods since diet proportions must total 100% to run the bioenergetics model.

We constructed a more detailed preyfish diet for walleye than for smallmouth bass or northern pikeminnow since walleye are highly piscivorous and previous research suggests only a small proportion of their diet is non-fish prey (Poe et al. 1991; Zimmerman 1999). The walleye diet consists of five prey categories: salmonids, American shad (AMS), sculpin, other fish, and miscellaneous (Table 7).

Table 6. The observed seasonal diet of smallmouth bass in LCRR compiled from several sources. A hypothetical diet without American shad was also developed. These diets were used to estimate the growth and potential salmonid consumption of smallmouth bass in LCRR using a bioenergetics model.

	Prey category (%)						
Time period	salmonids	AMS	other fish	crustaceans	miscellaneous		
	Estimate of cu	ırrent seasor	nal diet of sm	allmouth bass			
April/May	0	0	20	50	30		
June	0	0	34	62	4		
July	23	0	10	55	12		
Aug 1 – 14	16	15	10	55	4		
Aug $15 - 31$	0	15	23	58	4		
Sept/Oct	0	15	23	58	4		
Nov/Dec	0	10	0	40	50		
Н	ypothetical seas	sonal diet wi	ithout Americ	ean shad nrewf	ish		
April/May	0	0	20	50	30		
June	0	0	34	62	4		
July	23	0	10	55	12		
Aug 1 – 14	16	0	10	62	12		
Aug 15 – 31	0	0	26	62	12		
Sept/Oct	0	0	26	62	12		
Nov/Dec	0	0	10	40	50		
Proportion		-					
indigestible <sup>a</sup> :	0.033	0.0165	0.0165	0.1	0.4		

<sup>&</sup>lt;sup>a</sup> Stewart et al. (1983)

Sources: Poe et al. 1990; Shively et al. 1991; Tabor et al. 1994; Zimmerman 1999; Sauter, unpublished data.

Table 7. The observed seasonal diet of walleye in LCRR compiled from several sources. A hypothetical diet without American shad (AMS) was also developed. These diets were used to estimate the growth and potential salmonid consumption of walleye in LCRR using a bioenergetics model.

	Prey category (%)							
Time period	salmonids	AMS	sculpin	other fish	miscellaneous			
	Estima	te of current	seasonal diet c	of walleye				
April/May	20	0	50	20	10			
June	20	0	50	20	10			
July	20	0	50	20	10			
Aug 1 – 14	20	0	50	20	10			
Aug $15 - 31$	0	20	50	20	10			
Sept/Oct	0	20	50	20	10			
Nov/Dec	0	20	50	20	10			
	Hypothetical s	easonal diet	without Ameri	can shad preyfis	h			
April/May	20	0	50	20	10			
June	20	0	50	20	10			
July	20	0	50	20	10			
Aug 1 – 14	20	0	50	20	10			
Aug $15 - 31$	0	0	50	30	20			
Sept/Oct	0	0	50	30	20			
Nov/Dec	0	0	50	20	10			
Proportion								
indigestible <sup>a</sup> :	0.033	0.011	0.011	0.011	0.4			

<sup>&</sup>lt;sup>a</sup> Stewart et al. (1983)

Sources: Poe et al. 1991; Zimmerman 1999

#### Caloric density of prey

The caloric densities of various prey items in predator diets are an integral part of the bioenergetics model. The energy densities of many prey items consumed by aquatic predators in LCRR appear in Table 8. Our model used a caloric density of 5.56 kJ/g for juvenile American shad (Sauter and Petersen; Report C, in preparation) and a value of 4.31 kJ/g for juvenile salmonids (Rondorf et al. 1985). For the "other fish" proportion of the northern pikeminnow and smallmouth bass diets, which included sculpin, we used an energy density of 5.4 kJ/g. Sculpin constitute about 50% of the walleye diet in the spring and summer so we listed this species as a separate prey category in the walleye diet along with salmonids, American shad (AMS), other fish, and miscellaneous (Table 7). Since we placed sculpin, a preyfish with a relatively high caloric density into a separate diet category in the walleye diet, we reduced the caloric density of the other fish category to 4.1 kJ/g, a value similar to that of salmonids (Table 8) and in the mid-range of caloric densities listed for other preyfish (see Hanson 1997).

Table 8. The energy density (kJ/g) of common prey items of aquatic predators in the Columbia River basin

Species	Energy density	Source
	(kJ/g wet mass)	
Steelhead	4.61	Roby et al. (1998)
Chinook salmon	3.98	Roby et al. (1998)
Chinook salmon	4.31	Rondorf et al. (1985)
Coho salmon	5.04	Roby et al. (1998)
Sockeye salmon	5.07	Roby et al. (1998)
Sculpins	5.44	Rottiers and Tucker (1982);
		Brocksen et al. (1968)
American shad	5.67	Roby et al. (1998)
	5.56	Petersen and Sauter, Report C
		(in preparation)
Crayfish/crustaceans	4.51	Cummins and Wuycheck (1971)
Miscellaneous	2.62	Petersen and Ward (1999)

#### Water temperature

Water temperature and body mass regulate the basal metabolic rate, feeding rate, and digestion of fish, so temperature is an important component of bioenergetics modeling. We averaged 15 years of daily forebay scrollcase temperature records collected from 1980 – 1995 at John Day and Bonneville dams (<a href="www.cqs.washington.edu/dart/dart.html">www.cqs.washington.edu/dart/dart.html</a>) to create an annual profile of LCRR water temperatures for our modeling. The historic temperature model for the unimpounded free-flowing lower Columbia River was provided by Yearsley (1999) (Figure 1).

#### Availability of anadromous preyfish

Rearing and emigrating anadromous preyfish are present in the LCRR from early April through November (http://www.fpc.org). The annual emigration of anadromous fishes begins with the spring emigration of hatchery and wild juvenile salmon and steelhead in April; by mid-June, subyearling fall Chinook salmon are rearing and emigrating through the reservoirs, and juvenile American shad become abundant in early August. The emigration of juvenile American shad continues through much of the fall in the LCRR (Figure 2).

#### **Predator growth curves**

Data on the size-at-age of northern pikeminnow, smallmouth bass, and walleye in LCRR were available from previous research (see Beamsderfer and Ward 1994; Tinus and Beamsderfer 1994; Petersen, Report A, in preparation). We compiled additional size-at-age data from predator populations at other locations in the Pacific Northwest and North America to compare the growth rates of aquatic predators in the LCRR with fish collected at other locations.

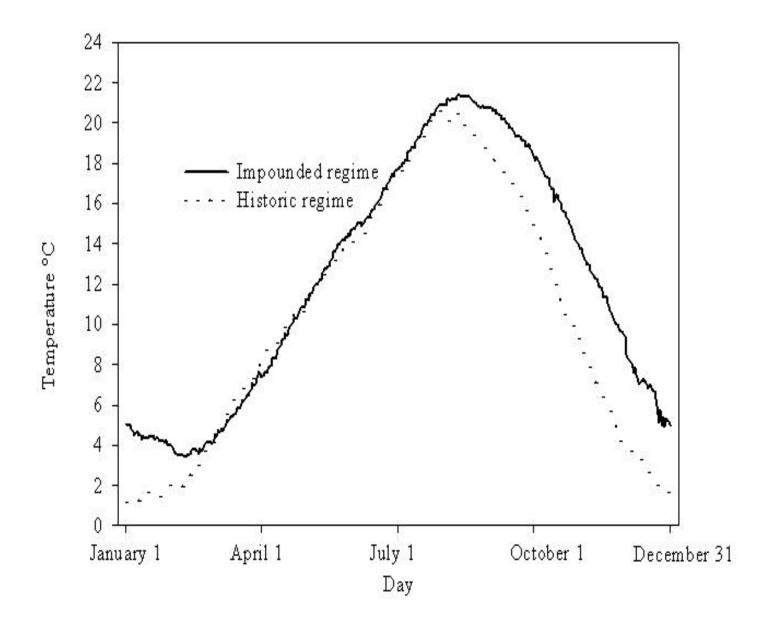


Figure 1. Impounded and historic water temperature profile of the LCRR showing (1) later peak summer water temperatures, (2) warmer peak summer water temperatures, and, (3) warmer fall and winter water temperatures under the impounded water temperature regime.

## Seasonal passage of juvenile anadromous fishes John Day Dam, 2000

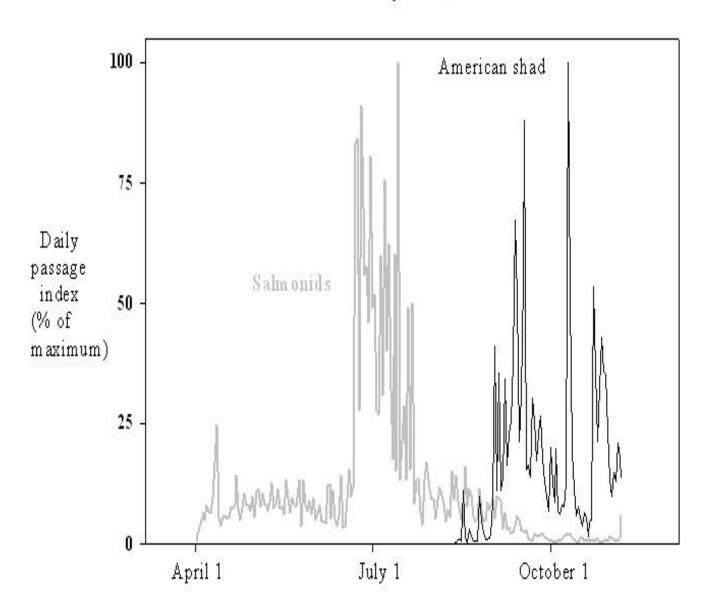


Figure 2. Seasonal passage of juvenile anadromous salmonids and American shad at John Day Dam in 2000. Passage counts were made at the John Day Dam fish collection facility and the index is relative to the maximum count for each species.

#### Results

#### **Bioenergetics**

For each predator species, we tested the hypothesis that a supplemental fall diet of juvenile American shad and reservoir water temperatures was equally important in producing the observed growth rates of aquatic predators in LCRR. Our bioenergetics simulations suggest that both the presence of American shad and higher water temperatures since impoundment are important to predator growth, but the growth contribution of these two factors varied by predator species.

The influence of American shad on smolt consumption varied by predator species in LCRR. A supplemental diet of American shad had a relatively small impact on northern pikeminnow (7.0%) and walleye (4.4%) smolt consumption, but produced a 16.1% increase in smallmouth bass consumption.

#### Northern pikeminnow

Simulations on northern pikeminnow suggest that while both American shad and impounded water temperatures are important growth factors for northern pikeminnow in LCRR, the observed diet of 25% American shad produced slightly greater annual increases in growth than water temperature alone (Table 9, simulation A). Comparison of the observed growth of northern pikeminnow under a fall diet of 25% American shad with the predicted growth of fish with no American shad in the fall diet and a fall diet of 25% American shad under historic water temperatures (simulation A versus B) suggests that American shad contribute as much or more to the observed annual growth of northern pikeminnow than water temperature. In fact, the warmest annual water temperatures each year may slow northern pikeminnow growth in LCRR (Petersen and Ward 1999). Simulation C which combined historic water temperatures without American shad in the diet predicted the slowest growth rates for northern pikeminnow. The presence of American shad in the fall diet of LCRR northern pikeminnow made a relatively small difference in the number of juvenile salmonids consumed by this predator (7.0%) (Table 11). Smolt consumption by northern pikeminnow declined by 10.8% under the combination of reduced growth and feeding opportunities.

#### Smallmouth bass

We predicted the growth of smallmouth bass in LCRR under three growth scenarios: (A) the current reservoir temperature regime and no American shad in the fall diet, (B) the historic temperature regime with 15% American shad in the fall diet, and (C) the historic temperature regime with no American shad in the fall diet. Our bioenergetics modeling on smallmouth bass suggests that the warmer water temperatures of the impounded LCRR have a much greater affect on the growth of this invasive predator than the presence of American shad (Table 10); however, the growth difference produced by a fall diet of 15% American shad under the reservoir water temperature regime increased smallmouth bass consumption of juvenile salmonids by 16.1% (Table 12). Our modeling suggests a much larger reduction in smolt consumption by smallmouth bass might occur if American shad were removed from the diet and this condition affected feeding opportunities (43.4%). Increased annual growth due to the warmer reservoir water temperatures has the greatest effect on the smaller size classes of smallmouth bass, which make up the largest proportion of the population. These bioenergetics results should be considered preliminary, since there were no fall field data available on which to base the fall diet of smallmouth bass in LCRR.

Table 9. Bioenergetics modeling comparing nominal annual growth (mass, g) with predicted growth of northern pikeminnow under four simulations: (A) current water temperatures without American shad (AMS) in the diet, (B) historic water temperatures and current fall diet conditions (25% AMS), and (C) historic water temperatures without AMS in the fall diet. The % change (%  $\Delta$ ) between the nominal and simulated growth is given for each scenario. To compare the current reservoir water temperature regime with historic conditions, see Figure 1. Temp = temperature.

		Northern pikeminnow simulations						
		•		-				
Non	ninal	A		В		C		
-		<u>A</u>		<u>D</u>		<u>C</u>		
Curren	t temps							
<u>&amp; 25%</u>	6 AMS	Current te	mps	Historic t	emps	Historic temps		
Starting	Final	No AMS	<u>S</u>	<u>&amp; 25% AMS</u>		& no AMS		
mass (g)	mass (g)	size (g)	$\%\Delta$	size (g)	$\%\Delta$	size (g)	$\%\Delta$	
100	219	186	-15.1	190	-13.2	167	-23.7	
400	543	489	-9.9	508	-6.4	469	-13.6	
750	876	806	-8.0	840	-4.1	789	-9.9	
1100	1197	1114	-6.9	1161	-3.0	1100	-8.1	
1400	1466	1373	-6.3	1431	-2.4	1363	-7.0	

Table 10. The nominal annual growth and interpolated nominal p-values for five starting sizes of smallmouth bass in LCRR. Simulations show the predicted final size of smallmouth bass under (A) current water temperatures (temp) without American shad in the fall diet (No AMS), (B) historic water temperatures with 15% American shad in the fall diet, and (C) historic water temperatures without American shad in the fall diet. The % change (%  $\Delta$ ) between the observed final size and simulation growth is given for each scenario. To compare the current water temperature regime with historic conditions, see Figure 1.

			Smallmouth bass simulations					
C	*	<u>A</u>		<u>B</u>		<u>C</u>		
	urrent tem 2 16% AN	<u>1S</u>	Current		Historic		Historic	
Start size (g)	Final size (g)	nominal p-value	temps & no AMS	% Δ	temps & 16% AMS	% Δ	temps & no AMS	% Δ
200	467	0.29589	448	-4.1	381	-18.4	369	-21.0
600	846	0.21681	825	-2.5	757	-10.5	742	-12.3
1000	1247	0.19636	1222	-2.0	1144	-8.3	1127	<b>-</b> 9.6
1200	1378	0.17304	1353	-1.8	1285	-6.7	1268	-8.0
1400	1503	0.15264	1481	-1.5	1421	-5.5	1405	-6.5

<sup>\*</sup> No field data are currently available on the fall diet of smallmouth bass. Our current growth model relied on a reasonable estimate of the fall diet of smallmouth bass.

Table 11. Cumulative predicted smolt consumption and percent change in consumption by LCRR northern pikeminnow under the current fall diet of 25% American shad and under a hypothetical diet without American shad. Age 1 and 2 northern pikeminnow cohorts consume few juvenile salmonids (x), and were not included in this analysis. Estimated average northern pikeminnow populations size in John Day Reservoir is also given. Pred = individual predator.

per 1000 fish         (g)         per pred (g)per pred (g)         per pred (g)	Predicted Northern pikeminnow smolt consumption									
Age         Population frequency per 1000 fish         mass (g)         salmon consumed per pred (g)         salmon consumed per per ochort (g)         mass (g)         American shad Growth effect salmon consumed per pred (g)         salmon consumed per per ochort (g)         x<										
Age         Population frequency per 1000 fish         mass consumed (g)         salmon consumed per pred (g)         salmon consumed per pred (g)         mass consumed per pred (g)         salmon consumed per cohort (g)         x						]				
Age         Population frequency per 1000 fish         wass (g)         salmon consumed oper pred (g) per cohort (g)         mass (g)         salmon consumed per pred (g) per cohort (g)         x				25% America	<u>n shad</u>					
Age         Population frequency per 1000 fish (g)         salmon consumed per pred (g) per cohort (g)         salmon consumed (g)         salmon consumed per pred (g) per cohort (g)         salmon consumed per per pred (g) per cohort (g)         salmon consumed per loop predators:         salmon consumed p							Growth et	<u>ffect</u>		
Age         frequency per 1000 fish         mass (g)         consumed per pred (g)         consumed per cohort (g)         consumed (g)         consumed per pred (g)         p										_
per 1000 fish         (g)         per pred (g)         per cohort (g)         per pred (g)		-								
1         x         x         x         x         x         x           2         x         x         x         x         x         x         x           3         2         126         35.7         71.4         104         35.7         71.4         35.0         70           4         15         228         61.8         927         196         52.9         793.5         55.9         838.5           5         40         350         89         3560         309         78.7         3148         78.3         3132           6         140         481         114.8         16072         431         103.7         14518         100.1         14014           7         100         616         138.8         13880         559         127.0         12700         121.2         12120           8         115         748         160.2         18423         684         148.1         17031.5         140.8         16192           9         140         874         179.2         25088         804         166.7         23338         158.6         22204           10         115         991	Age									
2         x         x         x         x         x         x         x           3         2         126         35.7         71.4         104         35.7         71.4         35.0         70           4         15         228         61.8         927         196         52.9         793.5         55.9         838.5           5         40         350         89         3560         309         78.7         3148         78.3         3132           6         140         481         114.8         16072         431         103.7         14518         100.1         14014           7         100         616         138.8         13880         559         127.0         12700         121.2         12120           8         115         748         160.2         18423         684         148.1         17031.5         140.8         16192           9         140         874         179.2         25088         804         166.7         23338         158.6         22204           10         115         991         195.8         22517         916         182.9         21033.5         174.7         20		per 1000 fish	(g)	per pred (g)	per cohort (g)	(g)	per pred (g)	per cohort (g)	per pred (g)	per cohort (g)
3         2         126         35.7         71.4         104         35.7         71.4         35.0         70           4         15         228         61.8         927         196         52.9         793.5         55.9         838.5           5         40         350         89         3560         309         78.7         3148         78.3         3132           6         140         481         114.8         16072         431         103.7         14518         100.1         14014           7         100         616         138.8         13880         559         127.0         12700         121.2         12120           8         115         748         160.2         18423         684         148.1         17031.5         140.8         16192           9         140         874         179.2         25088         804         166.7         23338         158.6         22204           10         115         991         195.8         22517         916         182.9         21033.5         174.7         20090.5           11         140         1098         210.1         29414         1019 <t< td=""><td>1</td><td>X</td><td>X</td><td>X</td><td>X</td><td>X</td><td></td><td></td><td>X</td><td>X</td></t<>	1	X	X	X	X	X			X	X
4         15         228         61.8         927         196         52.9         793.5         55.9         838.5           5         40         350         89         3560         309         78.7         3148         78.3         3132           6         140         481         114.8         16072         431         103.7         14518         100.1         14014           7         100         616         138.8         13880         559         127.0         12700         121.2         12120           8         115         748         160.2         18423         684         148.1         17031.5         140.8         16192           9         140         874         179.2         25088         804         166.7         23338         158.6         22204           10         115         991         195.8         22517         916         182.9         21033.5         174.7         20090.5           11         140         1098         210.1         29414         1019         197.1         27594         189.1         26474           12         90         1195         222.6         20034         1112 <td></td> <td>X</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td>		X								
5         40         350         89         3560         309         78.7         3148         78.3         3132           6         140         481         114.8         16072         431         103.7         14518         100.1         14014           7         100         616         138.8         13880         559         127.0         12700         121.2         12120           8         115         748         160.2         18423         684         148.1         17031.5         140.8         16192           9         140         874         179.2         25088         804         166.7         23338         158.6         22204           10         115         991         195.8         22517         916         182.9         21033.5         174.7         20090.5           11         140         1098         210.1         29414         1019         197.1         27594         189.1         26474           12         90         1195         222.6         20034         1112         209.5         18855         201.7         18153           13         65         1281         233.2         15158	3		126	35.7	71.4	104				
6         140         481         114.8         16072         431         103.7         14518         100.1         14014           7         100         616         138.8         13880         559         127.0         12700         121.2         12120           8         115         748         160.2         18423         684         148.1         17031.5         140.8         16192           9         140         874         179.2         25088         804         166.7         23338         158.6         22204           10         115         991         195.8         22517         916         182.9         21033.5         174.7         20090.5           11         140         1098         210.1         29414         1019         197.1         27594         189.1         26474           12         90         1195         222.6         20034         1112         209.5         18855         201.7         18153           13         65         1281         233.2         15158         1195         219.9         14293.5         212.8         13832           14         30         1358         242.4         7272	4	15	228	61.8	927	196	52.9	793.5	55.9	838.5
7         100         616         138.8         13880         559         127.0         12700         121.2         12120           8         115         748         160.2         18423         684         148.1         17031.5         140.8         16192           9         140         874         179.2         25088         804         166.7         23338         158.6         22204           10         115         991         195.8         22517         916         182.9         21033.5         174.7         20090.5           11         140         1098         210.1         29414         1019         197.1         27594         189.1         26474           12         90         1195         222.6         20034         1112         209.5         18855         201.7         18153           13         65         1281         233.2         15158         1195         219.9         14293.5         212.8         13832           14         30         1358         242.4         7272         1269         229.1         6873         222.5         6675           15         5         1425         250.2         1251	5	40	350	89	3560	309	78.7	3148	78.3	3132
8         115         748         160.2         18423         684         148.1         17031.5         140.8         16192           9         140         874         179.2         25088         804         166.7         23338         158.6         22204           10         115         991         195.8         22517         916         182.9         21033.5         174.7         20090.5           11         140         1098         210.1         29414         1019         197.1         27594         189.1         26474           12         90         1195         222.6         20034         1112         209.5         18855         201.7         18153           13         65         1281         233.2         15158         1195         219.9         14293.5         212.8         13832           14         30         1358         242.4         7272         1269         229.1         6873         222.5         6675           15         5         1425         250.2         1251         1334         236.7         1183.5         230.9         1154.5           16         3         1483         256.7         770.1	6	140	481	114.8	16072	431	103.7	14518	100.1	14014
9         140         874         179.2         25088         804         166.7         23338         158.6         22204           10         115         991         195.8         22517         916         182.9         21033.5         174.7         20090.5           11         140         1098         210.1         29414         1019         197.1         27594         189.1         26474           12         90         1195         222.6         20034         1112         209.5         18855         201.7         18153           13         65         1281         233.2         15158         1195         219.9         14293.5         212.8         13832           14         30         1358         242.4         7272         1269         229.1         6873         222.5         6675           15         5         1425         250.2         1251         1334         236.7         1183.5         230.9         1154.5           16         3         1483         256.7         770.1         1390         243.2         729.9         238.1         714.3            174,438         174,438         162,163	7	100	616	138.8	13880	559	127.0	12700	121.2	12120
10         115         991         195.8         22517         916         182.9         21033.5         174.7         20090.5           11         140         1098         210.1         29414         1019         197.1         27594         189.1         26474           12         90         1195         222.6         20034         1112         209.5         18855         201.7         18153           13         65         1281         233.2         15158         1195         219.9         14293.5         212.8         13832           14         30         1358         242.4         7272         1269         229.1         6873         222.5         6675           15         5         1425         250.2         1251         1334         236.7         1183.5         230.9         1154.5           16         3         1483         256.7         770.1         1390         243.2         729.9         238.1         714.3           Total salmon (g) consumed per 1000 predators:         174,438         162,163         155,664	8	115	748	160.2	18423	684	148.1	17031.5	140.8	16192
11         140         1098         210.1         29414         1019         197.1         27594         189.1         26474           12         90         1195         222.6         20034         1112         209.5         18855         201.7         18153           13         65         1281         233.2         15158         1195         219.9         14293.5         212.8         13832           14         30         1358         242.4         7272         1269         229.1         6873         222.5         6675           15         5         1425         250.2         1251         1334         236.7         1183.5         230.9         1154.5           16         3         1483         256.7         770.1         1390         243.2         729.9         238.1         714.3           Total salmon (g) consumed per 1000 predators:         174,438         162,163         155,664	9	140	874	179.2	25088	804	166.7	23338	158.6	22204
12         90         1195         222.6         20034         1112         209.5         18855         201.7         18153           13         65         1281         233.2         15158         1195         219.9         14293.5         212.8         13832           14         30         1358         242.4         7272         1269         229.1         6873         222.5         6675           15         5         1425         250.2         1251         1334         236.7         1183.5         230.9         1154.5           16         3         1483         256.7         770.1         1390         243.2         729.9         238.1         714.3           Total salmon (g) consumed per 1000 predators:         174,438         162,163         155,664	10	115	991	195.8	22517	916	182.9	21033.5	174.7	20090.5
13     65     1281     233.2     15158     1195     219.9     14293.5     212.8     13832       14     30     1358     242.4     7272     1269     229.1     6873     222.5     6675       15     5     1425     250.2     1251     1334     236.7     1183.5     230.9     1154.5       16     3     1483     256.7     770.1     1390     243.2     729.9     238.1     714.3       Total salmon (g) consumed per 1000 predators:     174,438     162,163     155,664	11	140	1098	210.1	29414	1019	197.1	27594	189.1	26474
14     30     1358     242.4     7272     1269     229.1     6873     222.5     6675       15     5     1425     250.2     1251     1334     236.7     1183.5     230.9     1154.5       16     3     1483     256.7     770.1     1390     243.2     729.9     238.1     714.3       Total salmon (g) consumed per 1000 predators:     174,438     162,163     155,664	12	90	1195	222.6	20034	1112	209.5	18855	201.7	18153
15     5     1425     250.2     1251     1334     236.7     1183.5     230.9     1154.5       16     3     1483     256.7     770.1     1390     243.2     729.9     238.1     714.3       Total salmon (g) consumed per 1000 predators:     174,438     162,163     155,664	13	65	1281	233.2	15158	1195	219.9	14293.5	212.8	13832
16     3     1483     256.7     770.1     1390     243.2     729.9     238.1     714.3       Total salmon (g) consumed per 1000 predators:     174,438     162,163     155,664	14	30	1358	242.4	7272	1269	229.1	6873	222.5	6675
Total salmon (g) consumed per 1000 predators: 174,438 162,163 155,664	15	5	1425	250.2	1251	1334	236.7	1183.5	230.9	1154.5
	16	3	1483	256.7	770.1	1390	243.2	729.9	238.1	714.3
	Total salmor	n (g) consumed p	oer 1000 p	oredators:	174,438			162,163		155,664
% change: -7.0 -10.8	% change:	·-·	•		·			-7.0		-10.8

<sup>&</sup>lt;sup>a</sup> Rieman et al. 1991

Table 12. Predicted salmonid consumption (g) by smallmouth bass in LCRR per individual predator (pred) and cohort. The % change in salmonid consumption attributed to faster growth from American shad in the fall diet compared to a diet without American shad is also given, along with the estimated average smallmouth bass population size in John Day Reservoir.

Predicted Smallmouth bass smolt consumption									
Estimated average population size in John Day Reservoir = 35,000 <sup>a</sup>									
		Reservoir diet with			Reservoir diet without			Reservoir diet without	
			15% America	n shad	American shad		American shad		
					Growth effect		Growth and reduced		
							<u>feeding effect</u>		
	Population		salmon	salmon		salmon	salmon	salmon	salmon
Age	frequency	mass	consumed	consumed	mass	consumed	consumed	consumed	consumed
	per 1000 fish	(g)	per pred (g)	per cohort (g)	(g)	per pred (g)	per cohort (g)	per pred (g)	per cohort (g)
1	X	X	X	X	X	X	X	X	X
2	643	98	7.2	4629.6	91	6.1	3922.3	4.5	2893.5
3	214	294	20.1	4301.4	279	16.5	3531	10.1	2161.4
4	71	550	32.2	2286.2	530	26.9	1909.9	16.2	1150.2
5	24	787	38.3	919.2	766	32.5	780	21.4	513.6
6	24	1053	46.6	1118.4	1028	39.8	955.2	26.8	643.2
7	12	1245	47.0	564	1221	40.3	483.6	30.6	367.2
8	6	1392	47.6	285.6	1369	41.0	246	33.4	200.4
9	3	1500	47.6	142.8	1477	41.1	123.3	35.4	106.2
10	3	1530	43.4	130.2	1509	37.6	112.8	36.0	108
Total salmon	Total salmon (g) consumed per 1000 predators:			14,377			12,064		8,143
% change:						-16.1		-43.4	

<sup>&</sup>lt;sup>a</sup> Rieman et al. 1991

#### Walleye

Bioenergetics modeling on walleye suggests that American shad are the most important factor contributing to the annual growth rate of this predator, particularly as walleye increase in size. Our simulations suggest that the availability of American shad in the late summer and fall as well as current reservoir water temperatures during the fall contribute to the annual growth rate of walleye in LCRR (Table 13). The predicted impact of walleye growth due to a 20% American shad fall diet under the impounded water temperature regime increased the estimated smolt consumption of walleye by 4.4% (Table 14). Our model predicted a 21.4% decrease in smolt consumption by walleye without American shad in the diet and under reduced feeding opportunities. These bioenergetics modeling results should be considered preliminary, since there were no fall field data available on which to base the fall diet of walleye in LCRR.

Table 13. The nominal annual growth and interpolated nominal p-values for five starting sizes of walleye in LCRR. Simulations show the predicted final size of walleye under (A) current water temperatures (temp) without American shad in the fall diet (No AMS), (B) historic water temperatures with 20% American shad in the fall diet, and (C) historic water temperatures without American shad in the fall diet. The % change (%  $\Delta$ ) between the observed final size and simulation growth is given for each scenario. To compare the current water temperature regime with historic conditions, see Figure 1.

			Walleye simulations					
]	Nominal*							
Current temps		<u>A</u>		<u>B</u>		<u>C</u>		
<u>&amp; 20% AMS</u>			Current	Historic Historic			Historic	
Starting	Final	growth	temps &		temps &		temps &	
mass (g)	mass (g)	p-value	no AMS	% Δ	20% AMS	% Δ	no AMS	% Δ
300	1574	0.49615	1417	-10.0	1365	-13.3	1248	-20.7
1000	1885	0.37137	1748	-7.3	1761	-6.6	1655	-12.2
3000	3621	0.32183	3428	-5.3	3515	-2.9	3361	-7.2
4000	4443	0.31144	4225	-4.9	4345	-2.2	4170	-6.1
5000	5391	0.31168	5140	-4.7	5286	-1.9	5084	-5.7

<sup>\*</sup> No field data are currently available on the fall diet of walleye. Our current growth model relied on a reasonable estimate of the fall diet of walleye.

#### **Predator Growth Curves**

Growth curves and a comparison of the size-at-age of 6 year-old predators for various locations suggest that growth conditions for northern pikeminnow (Figure 3, Table 15), smallmouth bass (Figure 4, Table 16), and walleye (Figure 5, Table 17) are quite favorable in LCRR. The average total length (TL, mm) of 6 year-old northern pikeminnow in LCRR (379 mm) is larger than the value reported for the lower Columbia River below Bonneville Dam (362 mm) or for other locations across the Pacific Northwest including Lake Washington, WA (359 mm) (Table 15). Although size-at-age information on smallmouth bass and walleye were only available for John Day Reservoir, data from these populations indicates 6 year-old predators are larger in this reservoir than at most other locations reported.

Table 14. Predicted salmonid consumption (g) by walleye in LCRR per individual predator (pred) and cohort. The % change in salmonid consumption attributed to faster growth from American shad in the fall diet compared to a diet without American shad is also given, as well as the estimated average walleye population size in John Day Reservoir.

Predicted Walleye smolt consumption									
Estimated average population size in John Day Reservoir = 10,000 <sup>a</sup>									
		Reservoir diet with			Reservoir diet without			Reservoir diet without	
		20% American shad			American shad			American shad	
					Growth effect		Growth and reduced		
									ng effect
	Population		salmon	salmon		salmon	salmon	salmon	salmon
Age	frequency	mass	consumed	consumed	mass	consumed	consumed	consumed	consumed
	per 1000 fish	(g)	per pred (g)	per cohort (g)	(g)	per pred (g)	* '-'	per pred (g)	per cohort (g)
1	102	182	9.6	979.2	149	9.6	979.2	0.1	10.2
2	72	925	135.4	9748.8	829	120.2	8654.4	37.6	2707.2
3	155	1794	289.9	44934.5	1661	269.5	41772.5	152.6	23653
4	251	2557	399.8	100350	2399	379.3	95204.3	270.6	67920.6
5	96	3201	481.4	46214.4	3023	460.6	44217.6	366.9	35222.4
6	140	3764	548.7	76818	3567	527.2	73808	444.6	62244
7	24	4214	598.9	14373.6	4005	576.8	13843.2	510.4	12249.6
8	45	4658	650.5	29272.5	4432	627.7	28246.5	562.1	25294.5
9	39	4978	682.7	26625.3	4745	659.2	25708.8	611.8	23860.2
10	79	5382	731.6	57796.4	5130	707.4	55884.6	647.7	51168.3
11	36	5498	733.2	26395.2	5253	708.8	25516.8	747.2	26899.2
12	45	5267	692.3	31153.5	5043	670.3	30163.5	703.2	31644
13	8	4195	529.5	4236	4040	513.3	4106.4	685.1	5480.8
	Total salmon (g) consumed per 1000 predators:			468,897			448,106		368,354
% change:							-4.4		-21.4

<sup>&</sup>lt;sup>a</sup> Rieman et al. 1991

Beamesderfer and Ward (1994) split their analysis of John Day Reservoir smallmouth bass size-at-age into upper and lower reservoir fish (Table 16). The average TL (mm) of 6 year-old upper reservoir fish (409 mm) was 11% larger than that of lower reservoir fish (364 mm). Smallmouth bass from upper John Day reservoir were also larger at age 6 than fish collected further upstream from a free-flowing section of the Columbia River at Hanford Reach, WA (380 mm) (Barfoot, unpublished data) and lower Snake River reservoirs (302 mm) but smaller than the reported size of 6 year-old smallmouth bass collected from 9 populations in California (462 mm) (Beamesderfer and North 1995).

Maule and Horton (1985) and Tinus and Beamesderfer (1994) report similar mean total lengths (TL, mm) for 6 year-old walleye in John Day Reservoir, although sampling occurred 10 years apart. Age 6 walleye appear to be growing faster in John Day Reservoir than fish sampled from many other locations in North America (Table 17) based on published data.

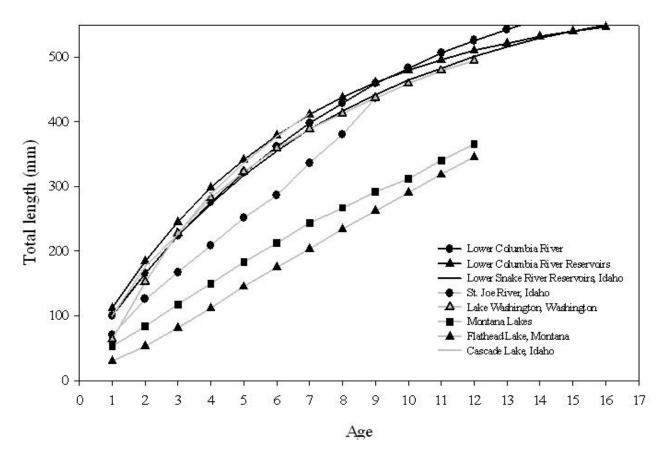


Figure 3. Growth curves for northern pikeminnow taken from various locations in the northwestern United States. "Lower Columbia River" refers to the free-flowing section downstream of Bonneville Dam. "Lower Columbia River reservoirs" refers to the impounded section of river between Bonneville and McNary dams. Sources: Casey 1962, Olney 1975, Petersen (Report A, in preparation). Original fork lengths (FL) were convert to total length (TL) using the relationship of FL to TL determined for Lake Washington northern pikeminnow by Olney 1975.

Table 15. Comparison of the size-at-age of 6 year-old northern pikeminnow reported for locations throughout the Pacific Northwest. Size-at-age is given as total length (TL, mm). Standard and fork length data was converted to TL using the equations of Olney (1975).

	Northern pikeminnow	
Location	Average TL (mm)	Reference
LCRR		Petersen Report A,
OR/WA	379	in preparation
Cascade Reservoir, ID	378	Casey 1962
Lower		Petersen Report A,
Columbia River, OR/WA	362	in preparation
		r ·r·····
Lake Washington, WA	359	Olney 1975
Lower Snake River		Petersen Report A,
Reservoirs, WA	355	in preparation
C. I. D. ID	20.6	D :11051
St. Joe River, ID	286	Reid 1971
Montana Lakes, MT	213	Peters 1964
Flathead Lake, MT	175	Rahrer 1963

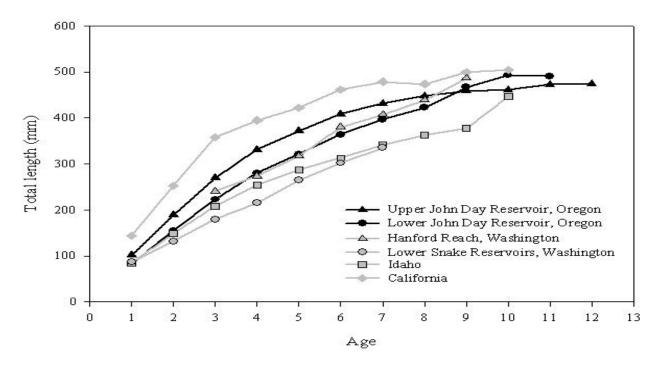


Figure 4. Growth curves for smallmouth bass taken from various locations in the United States. Fork lengths were converted to total length (x 1.04) as per Carlander, 1977. Sources: Barfoot (unpublished data); Beamesderfer and Ward 1994; Beamesderfer and North, 1995; Petersen et al. 1999.

Table 16. Comparison of the size-at-age of 6 year-old smallmouth bass reported for locations throughout the western United States. Size-at-age is given as total length (TL, mm).

Smallmouth bass

	Smannoum bass	
Location California	average TL (mm) 462	Reference Beamesderfer and North 1995
Upper John Day Reservoir, OR/WA	409	Beamesderfer and Ward 1994
Lower John Day Reservoir, OR/WA	364	Beamesderfer and Ward 1994
Hanford Reach, WA	380	Barfoot, unpublished data
Lower Snake River Reservoirs, WA	302	Barfoot, unpublished data
Idaho	313	Beamesderfer and North 1995

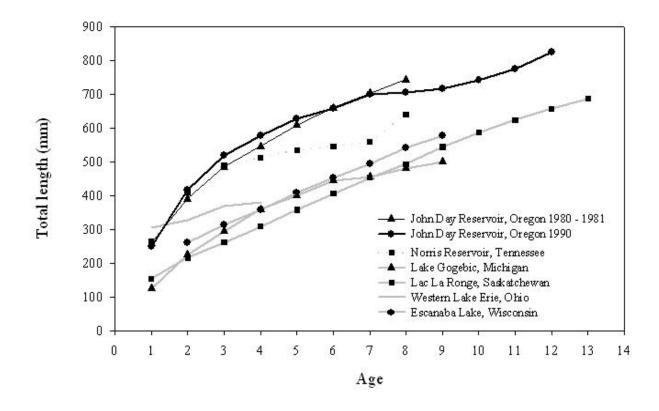


Figure 5. Growth curves for walleye in upper and lower John Day Reservoir of the lower Columbia River, and for other locations in the United States. Much of this data was summarized by Maule and Horton 1985. Sources: Eschmeyer 1950; Hartman and Margraf 1992; Kempinger and Carline 1977; Maule and Horton, 1995; Rawson, 1957; Serns 1984; Stroud 1949; Tinus and Beamesderfer 1994. Mass (g) of Western Lake Erie, Ohio walleye were converted to FL using the equation of Maule and Horton 1995; FL were converted to TL (x 1.06) as per Colby et al. 1979.

Table 17. Comparison of the size-at-age of 6 year-old walleye collected at locations throughout the western United States. Size-at-age is given as total length (TL, mm).

	Walleye	
Location	average TL (mm)	Reference
Upper John Day Reservoir 1980 - 1981	660	Maule and Horton 1985
John Day Reservoir 1990 - 1991	658	Tinus and Beamesderfer 1994
Norris Reservoir, TN	545	Stroud 1949
Escanaba Lake, WI	452	Kempinger and Carline 1977
Lake Gogebic, MI	445	Eschmeyer 1950
Western Lake Erie, OH	414	Hartman and Margraf 1992
Lac la Ronge, Canada	406	Rawson 1957

#### **Discussion**

In this study, we used bioenergetics modeling to look at two different aspects of aquatic predation on juvenile salmonids. The first portion of our work investigated the impact of juvenile American shad and the impounded water temperature regime on growth and salmonid consumption by northern pikeminnow in LCRR. The second portion of this study explored the impact of American shad and the impounded water temperature regime on the growth and salmonid consumption of two invasive predators in the reservoir system: smallmouth bass and walleye.

#### Northern pikeminnow predation

Our bioenergetics modeling suggests that important factors influencing the growth of northern pikeminnow in LCRR are the co-occurrence of large numbers of juvenile American shad and the warmer water temperatures of the impounded Columbia River during the fall. Petersen (Report A, in preparation) identified fish in the free-flowing Columbia River below Bonneville Dam as the fastest growing northern pikeminnow population in the lower Columbia River basin; other research reports that this location also has the greatest abundance of northern pikeminnow and the highest rate of northern pikeminnow predation on juvenile salmonids in the Columbia River system (Ward et al. 1995).

Our comparison of multiple growth curves from various northern pikeminnow populations indicates that LCRR fish grow faster than fish below Bonneville Dam for the first 9 years of life. Furthermore, the growth of northern pikeminnow below Bonneville Dam and in the LCRR exceeds that of other Pacific Northwest locations (Petersen Report A, in preparation). However, the growth rates observed in northern pikeminnow at these lower Columbia River locations apparently results from different foraging opportunities. Previous bioenergetics modeling by Sauter and Petersen (Report D, in

preparation) suggests that the high growth rate observed in northern pikeminnow below Bonneville Dam may be driven by large numbers of hatchery salmonids released into the lower Columbia River each spring and the presence of juvenile American shad in the fall. Sauter and Petersen (Report D, in preparation) estimated that juvenile salmonids historically represented about 35% of the northern pikeminnow diet below Bonneville Dam in the spring and summer compared to > 60% today. Their modeling predicted that under the historic proportion of juvenile salmonids (35%), the average mass (g) of 6 year-old northern pikeminnow would decrease by 8.6%, from 416 g to 380 g. By reducing the proportion of juvenile salmonids in the northern pikeminnow diet to 35% and eliminating American shad preyfish from the system, the model predicted the growth of 6 year-old northern pikeminnow below Bonneville Dam could be reduced by 17% from 416 g to 345 g (Sauter and Petersen, Report D, in preparation). Since 65% of the approximately 200 million anadromous hatchery salmon and steelhead produced in the Columbia River basin each year are released into the lower 175 miles of the Columbia River (Artificial Production Review and Evaluation (APRE), Draft 2003), it is not surprising that hatchery fish contribute substantially to northern pikeminnow growth below Bonneville Dam.

Anadromous preyfish are an important part of the northern pikeminnow diet in the LCRR as well. Hatchery salmonids make up  $\sim 40\%$  of the spring diet and large numbers of juvenile American shad contribute to the late summer and fall diet of northern pikeminnow in these reservoirs. The abundance of juvenile American shad during the late summer and fall may be particularly important to northern pikeminnow growth since the impounded water temperature regime has extended the annual growth period of aquatic predators later into the fall. The abundance of emigrating hatchery salmonids and introduced American shad, as well as favorable fall water temperatures all have a positive growth affect on northern pikeminnow in the LCRR.

The presence of juvenile American shad increases the annual growth of northern pikeminnow in LCRR, and this growth produced slightly greater smolt consumption (7.0%) than simulations predicting smolt consumption under a fall diet without American shad. However, our simulations suggest that if a diet without American shad also resulted in reduced feeding opportunities for northern pikeminnow, the decrease in smolt consumption by this predator might be greater (-10.8%). The slight increase in northern pikeminnow smolt consumption produced by the current fall diet rich in American shad suggests no single dietary component exerts a dominant effect on northern pikeminnow growth in LCRR. Northern pikeminnow are omnivorous, and known to switch prey throughout the growing season (Poe et al. 1991; Zimmerman 1999); they also respond quickly to the feeding opportunities presented by high densities of anadromous preyfish (Collis et al. 1995; Shively et al. 1996) but search out a variety of abundant high-quality prey when anadromous preyfishes are temporally or spatially scarce (Poe et al. 1991; Petersen and DeAngelis 1992; Zimmerman 1999). Prickly sculpin (Cottus asper) and crayfish are both important components of the northern pikeminnow diet in the LCRR, and are energetically comparable to anadromous preyfish (Poe et al. 1991; Zimmerman 1999; Sauter and Petersen, Report C, in preparation).

#### **Invasive Predators**

The second portion of our study dealt with the impact of juvenile American shad on populations of invasive predators. Bioenergetic modeling on smallmouth bass and walleye suggests that the impounded water temperature regime is the most critical factor supporting the growth rates of these invasive predators in LCRR. Because there is less information available on the late summer and fall diets of these invasive predators, the impact of juvenile American shad on the growth and salmonid consumption of smallmouth bass and walleye is less certain. For our bioenergetics modeling we assumed that the well documented proportion of juvenile salmonids (primarily subyearling fall Chinook) in the diet of the predators during the summer (Poe et al. 1991; Shively et al. 1991; Zimmerman 1999) provided a good

indication of the proportion of American shad in predator diets during the late summer and fall. Since juvenile salmonids and American shad temporally overlap in late summer, we structured predator diets for our simulations so that juvenile American shad became available to predators in early August and replaced the proportion of juvenile salmonids in predator diets by mid-August. The overall abundance of juvenile American shad and subyearling fall Chinook passing John Day Dam is similar in August, with the number of juvenile American shad increasing as subyearling fall Chinook decline during the month. Finally, the shoreline feeding behavior of subyearling fall Chinook (Mains and Smith 1956; Dauble et al. 1989; Poe et al. 1994) and larval and juvenile American shad (Miller 1993; Limburg 1996; Petersen et al. 2003) supports the use of similar dietary proportions for these two anadromous prey species in invasive predator diets.

Although there are varying degrees of uncertainty about the late summer and fall diet proportions of invasive aquatic predators in LCRR, previous researchers have found evidence that these predators encounter and consume larval and juvenile American shad (Zimmerman 1999; Petersen et al. 2003) and emigrating salmonids (Poe et al. 1991; Shively et al. 1991; Vigg et al. 1991; Zimmerman 1999). Overall, our modeling attributes 27.5% of the salmonid consumption in LCRR to faster growth rates of northern pikeminnow, smallmouth bass, and walleye foraging on juvenile American shad. Our simulations suggest that greater reductions in smolt consumption by predators might occur if the elimination of American shad from the reservoirs reduces the feeding opportunities of predators as well as their growth. The partitioning of food resources between northern pikeminnow, smallmouth bass, and walleye in LCRR, although unknown, may be quite dynamic. Substantial reductions in the availability of American shad may reduce the growth of predator populations and result in significant dietary shifts if competition for preyfish between predators increased.

#### Smallmouth bass

The inshore feeding pattern and use of mainstem shoreline, sloughs, and backwater habitats by juvenile American shad (Miller 1993; Limburg 1996; Petersen et al. 2003) provides good evidence for the spatial and temporal habitat overlap of American shad preyfish and smallmouth bass in LCRR. Smallmouth bass are recognized as an important predator on juvenile American shad on the east coast of North America where American shad are a native species (Johnson and Dropkin 1992; Johnson and Ringler 1995).

Bioenergetics simulations suggest that while a late summer and fall diet of American shad produces a minor increase in smallmouth bass growth, the indirect result of this growth in terms of the proportion of salmonids consumed by smallmouth bass is potentially quite large. Tabor et al. (1993) and other authors suggested that smallmouth bass consume large numbers of salmonid prey whenever the preferred habitat of smallmouth bass overlaps with subvearling fall Chinook rearing (Gray and Rondorf 1986; Curet 1993; Poe et al. 1994; Zimmerman 1999) and the abundance of juvenile salmonids is high (Warner 1972; Pflug and Pauley 1984). In fact, Tabor et al. (1993) found that the smallmouth bass diet consisted of 59% (by weight) subvearling fall Chinook in the upper portion of McNary Reservoir during the late spring and early summer. Research on LCRR smallmouth bass populations provides further evidence that the impact of this invasive predator on subyearling fall Chinook could be quite high and indirectly linked to the abundance of juvenile American shad. A study in John Day Reservoir by Vigg et al. (1991) noted that the mean daily preyfish ration of smallmouth bass is about twice that of other aquatic predators. This same study described the reservoir diet of smallmouth bass > 200 mm as 82% fish. Smallmouth bass as small as 75 mm have been observed with salmonid prey in their stomach contents (Beamsderfer and Ward 1994); these small bass will probably consume larval, and juvenile American shad as well. And, although small individuals consume less prey than larger predators, 1 and 2 year old smallmouth bass make up a substantial proportion of the population in the LCRR (Zimmerman

and Parker 1995) and may contribute significantly to salmonid losses. Our bioenergetics work on smallmouth bass suggests this predator may contribute to the poor survival observed in subyearling fall Chinook migrating through the reservoir system in July and August (Conner et al. 1998; Muir et al. 1998; Connor et al. 2001; Smith et al. 2003; Tiffan et al. 2003). Vigg et al. (1991) report that smallmouth bass consumption of juvenile salmonids peaks in July and remains high through August, while consumption is declining during August in northern pikeminnow, walleye, and channel catfish. Although the reduced survival of late migrating subyearling fall Chinook through the reservoir system may be due directly to stress associated with high water temperatures (Coutant 1999; Mesa 2002), indirect effects of exposure to high water temperatures include increased predation mortality (Vigg and Burley 1991; Marine and Cech 2004), higher incidence of disease (Fryer and Pilcher 1974), and substantial increases in passage mortality at hydropower facilities (Muir et al. 1998; Perry et al. 2003).

As part of a study on turbine passage mortality of subyearling fall Chinook, Perry et al. (2003) released radio-tagged fish into McNary Dam tailrace and estimated their survival through the upper portion of John Day Reservoir. Upper John Day Reservoir has relatively high shoreline habitat complexity, including islands, mainstem shorelines, shallow marshes, backwaters, and sloughs that extend 46 km downstream of McNary Dam tailrace to Crow Butte. Large numbers of smallmouth bass use the extensive backwater areas (Beamsderfer and Ward 1994), and juvenile salmonids and American shad are also attracted to the varied shoreline habitat of this reach (Barfoot et al. 2002). Radio-tagged subyearling fall Chinook suffered 33.6% mortality migrating through upper John Day Reservoir (Perry, personal communication). Some of the loss reported for these subyearling fall Chinook was probably due directly to stress from tagging and high water temperatures (near 23.5° C), but predation, particularly by smallmouth bass, may also be an important factor contributing to this high mortality.

Other research suggests smallmouth bass predation may not be limited to natural shoreline areas. A study by Duran et al. (2003) investigated the movements of radio-tagged northern pikeminnow and smallmouth bass in The Dalles Dam tailrace, an area with rocky shorelines, numerous bedrock islands, and backwater areas associated with the structural configuration of the dam. Although the predators that ingested radio-tagged juvenile salmonids could not be differentiated by species, Duran et al. (2003) found that the proportion of tagged juvenile salmonids ingested by northern pikeminnow and smallmouth bass increased between spring (2%) and summer (7%). Both predator species preferred bedrock substrate and shallow, low velocity water near structure. Despite their preference for the bedrock islands, artificial backwaters, and shoreline habitat, radio-tagged smallmouth bass were occasionally located further off-shore in the sluiceway zone where large numbers of juvenile salmonids concentrated. The study by Duran et al. (2003) suggests that juvenile salmonids are vulnerable to smallmouth bass predation whenever natural or artificial structures and flow patterns take migrating fish near shoreline areas.

#### Walleye

Bioenergetics modeling to assess the contribution of juvenile American shad towards the growth and salmonid consumption of walleye in LCRR produced results opposite from that of smallmouth bass. Our results suggest that juvenile American shad may be particularly important in explaining the high growth rate of walleye observed in LCRR, but this growth did not result in a large increase in salmonid consumption (+4.4%). Walleye are highly piscivorous in LCRR (Zimmerman 1999); nearly all of the prey (by weight) consumed by walleye in John Day Reservoir are fish (Poe et al. 1991). Zimmerman (1999) reported similar diet results for walleye at reservoir locations throughout the lower Columbia River basin. Like smallmouth bass, walleye show an exponential increase in the proportion of preyfish consumed between April and July (Vigg et al. 1991), and juvenile salmonids as well as American shad have been observed in the walleye diet (Gray et al. 1984; Maule and Horton 1984; Poe et al. 1988).

Our bioenergetics simulations suggest that juvenile American shad enhance walleye growth, but the proportion of salmonid consumption attributed to this growth was less for walleye (4.4%) than for either smallmouth bass (16.1%) or northern pikeminnow (7.0%). Based on the data available to us on population size, and our assumptions on the proportion of juvenile American shad in the walleye diet, the impact of American shad preyfish on walleye consumption of juvenile salmonids appears to be low in the LCRR (Beamsderfer and Rieman 1991; Zimmerman and Parker 1995).

#### Impact of juvenile American shad

Our bioenergetics modeling suggests that invasive American shad contribute to the growth of native and invasive aquatic predators in the LCRR, and that this growth increases the consumption of juvenile salmonids by northern pikeminnow, smallmouth bass, and walleye. The abundance of American shad in the late summer/fall diet of predators probably indirectly increases predator consumption of juvenile salmonids by increasing the growth and size of predator populations.

In this study, bioenergetics simulations predicted reduced growth and lower salmonid consumption by northern pikeminnow, smallmouth bass, and walleye in model runs without juvenile American shad in predator diets. Increased predator growth due to American shad may be the result of the high caloric density of juvenile American shad compared to alternative prey types, and/or increased foraging efficiency on shoaling juvenile American shad. We kept the feeding rate of predator cohorts constant in our growth models whether juvenile American shad were present or not. This approach assumes that predator cohorts consume similar proportions but less energetically profitable prey when American shad preyfish are not available. This assumption may or may not be correct. In bioenergetics modeling of northern pikeminnow growth in the lower Snake River, where there are relatively low numbers of anadromous preyfish, Sauter and Petersen (Report C, in preparation) used higher p-value estimates in simulations with large numbers of anadromous preyfish in the northern pikeminnow diet, arguing that the density of migrating preyfish fundamentally affects northern pikeminnow feeding behavior and growth. Many predators, including northern pikeminnow, appear to adjust their foraging behavior in response to changing prey density (Krebs and Kacelnik 1984; Lucas 1990; Petersen and DeAngelis 1992). Predators may feed rapidly and consume a larger ration of food when prey density is high (Tyler and Dunn 1976; Grove et al. 1978; Jobling 1982; Miglavs and Jobling 1989; Petersen and DeAngelis 1992), and this functional response may result in spatial differences in the size, density, and aggregation of northern pikeminnow (Petersen 2001).

Alternatively, the feeding rate of predators might be expected to decrease if highly aggregated American shad preyfish were not available to predators, in which case the difference between predator growth and salmonid consumption with and without juvenile American shad in the fall diet would increase. It is unlikely that the feeding rate of predators would rise in response to a diet without juvenile American shad because predators would have to increase their foraging activity on less aggregated, and perhaps less energy-rich prey, and intra- and inter-specific competition for preyfish might increase between predators. Our modeling assumption that the feeding rate of predator cohorts remains constant whether juvenile American shad are present or not, gives the most conservative estimate of differences in predator growth and salmonid consumption between the two fall diet conditions. When considering the smolt consumption of predators without American shad in their diets, we included bioenergetics runs that modeled reduced feeding opportunities and growth in our estimates. Under these conditions, predicted smolt consumption by predators decreased dramatically. However, some authors have suggested that large numbers of anadromous preyfish do not affect the feeding behavior of smallmouth bass and walleye (Poe et al. 1991).

Juvenile American shad may be a particularly easy source of food for aquatic predators near lower Columbia River dams, where emigrating fish suffer high stress-related mortality from delayed migration,

confinement in fish passage facilities, dam passage, high water temperatures, and reduced predator avoidance (Shrimpton et al. 2001). Freshly dead preyfish offer as much energy to predators as live fish (Gadomski and Hall-Griswold 1992), and this non-evasive prey is easily captured and may settle in areas of lower water velocity preferred by northern pikeminnow (Faler et al. 1988; Duran et al. 2003) and smallmouth bass (Sechnick et al. 1986; Todd and Rabeni 1989; Duran et al. 2003). Many predators use prey movement as a feeding cue (Ware 1972; Howick and O'Brien 1983; Irvine and Northcote 1983; Luczkovich 1988); however, northern pikeminnow preferentially fed on dead juvenile salmonids in laboratory experiments (Gadomski and Hall-Griswold 1992), and showed significant selection for dead juvenile salmonids in Bonneville Dam tailrace as well (Petersen et al. 1994). Petersen et al. (1994) also reports a very high proportion of American shad in the diet of northern pikeminnow during one year of the study at Bonneville Dam. Differences in the proportion of American shad in the northern pikeminnow diet at Bonneville Dam between years is probably linked to the abundance and timing of the American shad emigration which was much greater during the 1990 study period than in 1991 (Petersen et al. 1994). Although the response of smallmouth bass, and walleye to dead preyfish has not been investigated, the prevalence of injured and dead juvenile American shad near dam sites may contribute to the growth and increased salmonid consumption of invasive predators.

#### **Conclusions**

Northern pikeminnow, smallmouth bass, and walleye all display high growth rates in the LCRR. Petersen et al. (2003) suggests that faster growing predator populations may produce more offspring and consume a greater proportion of juvenile salmonids than slower growing populations. Identifying the prey species and environmental conditions that contribute to the growth of predators is important in planning and implementing strategies to reduce the impact of these predators on juvenile salmonids. Although northern pikeminnow predation has received the most attention, invasive predators are also known to consume large numbers of juvenile salmonids in LCRR (Poe et al. 1991; Rieman et al. 1991; Vigg et al. 1991; Tabor et al. 1993; Zimmerman 1999). Previous studies also found indications that juvenile American shad might contribute to the growth of these predators (Gray et al. 1984; Maule and Horton 1984; Poe et al. 1988; Poe et al. 1991; Johnson and Ringler 1995; Johnson and Dropkin 1992). In this study, we identified juvenile American shad, an invasive preyfish, as an important prey species contributing to the growth of northern pikeminnow in LCRR. Bioenergetics modeling suggests that American shad are also a potentially important prey species contributing to the growth and salmonid consumption of invasive predators, particularly smallmouth bass, but better information on the feeding behavior and seasonal diets of these predators is needed.

The role of American shad in the growth and salmonid consumption of aquatic predators in LCRR is not surprising given the timing of the American shad emigration. The late summer and fall emigration of juvenile American shad provides an abundant source of anadromous preyfish for predators at a time when there are few juvenile salmonids available. The abundance of juvenile American shad and the warmer fall water temperatures of the LCRR creates opportunities for feeding and growth of predator populations that otherwise would not exist. If dam passage is associated with high levels of stress-related mortality in juvenile American shad as the laboratory research by Shrimpton et al. (2001) suggests, American shad may be a particularly easy source of high-quality food for aquatic predators. Research on the dam passage mortality of juvenile American shad, and the feeding responses of smallmouth bass and walleye to dead preyfish would offer important insights on predation issues near dams.

Smallmouth bass may be especially important when considering subyearling fall Chinook survival (Perry et al. 2003) for the following reasons: (1) smallmouth bass maintain a higher maximum daily ration later in the summer than the other aquatic predators (Vigg et al. 1991), (2) there appears to be more extensive temporal and spatial overlap between the preferred habitat of smallmouth bass and the rearing

habitat of subyearling fall Chinook and larval and juvenile American shad than with the other aquatic predators (Gray and Rondorf 1986; Petersen et al. 2003), (3) although our bioenergetics modeling suggests that larval and juvenile American shad have a limited effect on smallmouth bass growth, this growth translated into a substantial amount (16.1%) of salmonid consumption, (4) smallmouth bass are the second most abundant predator in John Day Reservoir and are most abundant in the impounded areas of the lower Columbia River (Beamsderfer and Rieman 1991; Zimmerman and Parker 1995), and (5) although northern pikeminnow are more abundant than smallmouth bass in the reservoir system, the peak summer water temperatures observed in the reservoirs (~22 °C) may reduce the feeding rate of northern pikeminnow during this period while increasing the feeding rate of smallmouth bass (Petersen and Ward 1999).

Because water temperatures remain cool in LCRR throughout much of the spring smolt migration, we concluded that northern pikeminnow are the most important source of predation mortality on juvenile salmonids. The growth and predation potential of smallmouth bass, walleye, and channel catfish is constrained by water temperatures during much of the spring emigration. For this reason, invasive predators in the LCRR may be a greater threat to subyearling fall Chinook than to other salmonids. The earliest portion of the subyearling fall Chinook emigration begins to move into the lower Columbia river reservoirs in mid-June. This portion of the emigration is primarily hatchery fish released from Priest Rapids hatchery (Tiffan et al. 2003). Later migrants are primarily wild fish from the Hanford Reach and Snake River. The nearshore feeding and migration pattern, smaller size, and slower migration of wild subyearling fall Chinook (Haskell et al. 2001; Tiffan et al. 2003) combined with warmer late spring and summer water temperatures in the reservoirs probably make this salmonid species more vulnerable than spring migrants to invasive predator species. However, juvenile salmonids are susceptible to invasive predators whenever flow patterns take emigrants along shorelines or into structurally complex habitat and lower velocity waters.

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### References

- Artificial Production Review and Evaluation. 2003. Draft Basin-Level Report, Document 2003-17, Northwest Power and Conservation Council, October 7, 2003.
- Armour, C.. 1993a. Evaluating temperature regimes for protection of smallmouth bass. USDI, Fish and Wildlife Service, National Biological Survey, Resource Publication 191, Washington, D.C.
- Armour, C.. 1993b. Evaluating temperature regimes for protection of walleye. USDI, Fish and Wildlife Service, National Biological Survey, Resource Publication 195, Washington, D.C.
- Barfoot, C.A., D.M. Gadomski, and J.H. Petersen. 2002. Resident fish assemblages in shallow shorelines of a Columbia River impoundment. Northwest Science 76(2):103-117.
- Beamesderfer, R.C., B.E. Rieman, L.J. Bledsoe, and S. Vigg. 1990. Management implications of a model of predation by a resident fish on juvenile salmonids migrating through a Columbia River reservoir. North American Journal of Fisheries Management 10:290-304.
- Beamesderfer, R.C., and B.E. Rieman. 1991. Abundance and distribution of northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:439-447.
- Beamesderfer, R.C. and D.L. Ward. 1994. Review of the status, biology, and alternatives for management of smallmouth bass in John Day Reservoir. Oregon Dept. of Fish and Wildlife Information Reports # 94-4.
- Beamesderfer, R.C. and J.A. North. 1995. Growth, natural mortality, and predicted response to fishing for largemouth bass and smallmouth bass populations in North America. North American Journal of Fisheries Management 15:688-704.
- Beamesderfer, R. C., D. L. Ward, and A. A. Nigro. 1996. Evaluation of the biological basis for a predator control program on northern squawfish (*Ptychocheilus oregonensis*) in the Columbia and Snake rivers. Canadian Journal of Fisheries and Aquatic Sciences 53:2898-2908.
- Brocksen, R.W., G.E. Davis, and C.E. Warren. 1968. Competition, food consumption, and production of sculpins and trout in laboratory stream communities. Journal of Wildlife Management 32:51-75.
- Brown, L.R. and P.B. Moyle. 1981. The impact of squawfish on salmonid populations: a review. North American Journal of Fisheries Management 1: 104 111.
- Carlander, K.D.. 1977. Handbook of freshwater fishery biology, volume 2. Iowa State University Press, Ames.
- Casey, O.E. 1962. The life history of the northern squawfish in Cascade Reservoir. M.S. Thesis, University of Idaho, Moscow. 47 p.
- Colby, P.J, R.E. McNicol, and R.A. Ryder. 1979. Synopsis of biological data on the walleye, Stizostedion vitreum vitreum (Mitchell 1818). FAO Fish. Synop. 119, 139 p.
- Collis, K., R.E. Beaty, and B.R. Crain. 1995. Changes in catch rate and diet of northern pikeminnow associated with the release of hatchery-reared juvenile salmonids in a Columbia River reservoir. North American Journal of Fisheries Management 15:346-357.
- Conner, W.P., H.L. Burge, and D.H. Bennett. 1998. Detection of PIT-tagged subyearling chinook salmon at a Snake River dam: implications for summer flow augmentation. North American Journal of Fisheries Management 18:530-536.
- Conner, W.P. 2001. Juvenile life history, downstream migration rate, and survival of wild Snake River fall chinook salmon. Ph.D. dissertation, University of Idaho, Moscow. 117 p.
- Coutant, C.C. 1999. Perspectives on temperature in the Pacific Northwest's fresh waters. Oak Ridge National Laboratory, Environmental Sciences Division, Publication No. 4849.

- Cummins, K. W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Mitteilungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 18.
- Curet, T.S. 1993. Habitat use, food habits, and the influence of predation on subyearling chinook salmon in Lower Granite and Little Goose Reservoirs, Washington. Master of Science Thesis, University of Idaho, Moscow. 70 p.
- Dauble, D.D., T.L. Page, and R.W. Hanf, Jr. 1989. Spatial distribution of juvenile salmonids in the Hanford Reach, Columbia River. U.S. National Marine Fisheries Service Fishery Bulletin 87:775-790.
- Duran, I.N., T.L. Liedtke, and J.H. Petersen. 2003. Predator-Prey interactions in The Dalles Dam tailrace, 2002. Annual report of research. U.S. Army Corps of Engineers, Portland, Oregon.
- Eschmeyer, P.H.. 1950. The life history of the walleye, (<u>Stizostedion vitreum vitreum (Mitchell)</u>), in Michigan. Michigan Dept. Conserv., Bull. Inst. Fish. Sci. 3.
- Faler, M.P., L.M. Miller, and K.I. Welke. 1988. Effects of variations in flow on distribution of northern squawfish in the Columbia River below NcNary Dam. North American Journal of Fisheries Management 8:30-35.
- Fryer, J.S., and K.S. Pilcher. 1974. Effects of temperature on diseases of salmonid fishes. U.S. Environmental Agency, Ecological Research Series EPA-660/3-73-020, Washington, D.C.
- Gadomski, D.M. and J.A. Hall-Griswold. 1992. Predation by northern squawfish on live and dead juvenile chinook salmon. Transactions of the American Fisheries Society. 121:680-685.
- Gray, G.A., D.E. Palmer, B.L. Hilton, R.J. Connolly, H.C. Hansel, and J.M. Beyer. 1984. Feeding activity, rate of consumption, daily ration and prey selection of major predators in John Day pool. Annual Report to the Bonneville Power Administration. Portland, Oregon.
- Gray, G.A. and D.W. Rondorf. 1986. Predation on juvenile salmonids in Columbia Basin reservoirs. Pages 178–185 *in* G.E. Hall and M.J. Van Den Avyle, editors. Reservoir Fisheries Management: Strategies for the 80's. American Fisheries Society, Southern Division, Reservoir Committee, Bethesda, Maryland.
- Grove, D.J., L. G. Lorizides, and J. Nott. 1978. Satiation amount, frequency of feeding and gastric emptying rate in <u>Salmo gairdneri</u>. Journal of Fish Biology. 12:507-516.
- Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Bioenergetics Model 3.0 for Windows. University of Wisconsin Sea Grant Institute, Technical Report WISCU-T-97-001, Madison.
- Haskell, C.A., D.W. Rondorf, and K.F. Tiffan. 2001. Community, temporal, and spatial dynamics of zooplankton in McNary and John Day reservoirs, Columbia River. Pages 107-133 *In* K.F. Tiffan, D.W. Rondorf, W.P. Connor, and H.L. Burge, (eds.). Post-release attributes and survival of hatchery and natural fall chinook salmon in the Snake River. Bonneville Power Administration, Annual Report 1999. Portland, OR.
- Hartman, K.J. and F.J. Margraf. 1992. Effects of prey and predator abundances on prey consumption and growth of walleyes in Western Lake Erie. Transactions of the American Fisheries Society 121: 245 260.
- Howick, G.L. and W.J. O'Brian. 1983. Piscivorous feeding behavior of largelmouth bassL an experimental analysis. Transactions of the American Fisheries Society 112:508-516.
- Irvine, J.R. and T.G. Northcote. 1983. Selection by young rainbow trout (*Salmo gairdneri*) in simulated stream environments for live and dead prey of different sizes. Canadian Journal of Fisheries and Aquatic Sciences 40:1745-1749.
- Jobling, M.. 1982. Some observations on the effects of feeding frequency on the food intake and growth of plaice. Journal of Fish Biology 19:439-455.

- Johnson, J.H. and D.S. Dropkin. 1992. Predation on recently released larval American shad in the Susquehanna River basin. North American Journal of Fisheries Management 12:504-508.
- Johnson, J.H. and N.H. Ringler. 1995. Estimating losses to predation of recently released American shad larvae in the Juniata River, Pennsylvania. North American Journal of Fisheries Management 15:854-861.
- Kempinger, J.J. and R.F. Carline. 1977. Dynamics of the walleye (*Stizostedion vitreum vitreum*) population in Escanaba Lake, Wisconsin, 1955 72. Journal of the Fisheries Research Board of Canada 34: 1800 -1811.
- Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). Journal of the Fisheries Research Board of Canada 34:1922-1935.
- Knutsen, C.J. and D.L.Ward. 1997. Biological characteristics of northern squawfish in the lower Columbia and Snake rivers, before and after sustained exploitation. *In*: D.L. Ward (ed.), Evaluation of the northern squawfish management program. Final report of research, 1990 1996. Bonneville Power Administration, Portland, Oregon.
- Krebs, J.R., and A., Kacelnik. 1984. Time horizons of foraging animals. Annals of the New York Academy of Sciences 423:278-291.
- Limburg, K.E.. 1996. Growth and migration of 0-year American shad (*Alosa sapidissima*) in the Hudson River estuary: otolith microstructural analysis. Canadian Journal of Fish and Aquatic Sciences 53: 220- 238.
- Lucas, J. R.. 1990. Time scale and diet choice decisions. P. 165-185. *In* R.N. Hughes (ed.) Behavioural mechanisms of food selection. NATO ASI Series, Subseries G. Springer Verlag, Heidelberg.
- Luczkovich, J.J. 1988. The role of prey detection in the selection of prey by pinfish *Lagodon rhomboids* (Linnaeus). Journal of Experimental Marine Biology and Ecology 123: 15-30.
- Lukas, J.A. and D.J. Orth. 1995. Factors affecting the nesting success of smallmouth bass in a regulated Virginia stream. Transactions of the American Fisheries Society 124: 726 735.
- Mains, E.M. and J.M. Smith. 1956. The distribution, size, time, and current preferences of seaward migrant chinook salmon in the Columbia and Snake rivers. Washington State Dept. of Fisheries report to U.S. Army Corps of Engineers, Contract DQ- 35026-Eng-20571. Walla Walla, Washington.
- Marine, K.R. and J.J. Cech, Jr. 2004. Effects of high water temperature on growth, smoltification, and predator avoidance in juvenile Sacramento River Chinook salmon. North American Journal of Fisheries Management. 24: 198 210.
- Maule, A.G. and H.F. Horton. 1984. Feeding ecology of walleye, (*Stizostedion vitreum vitreum*), in the mid-Columbia River, with emphasis on the interactions between walleye and juvenile anadromous fishes. Fishery Bulletin 82: 411-418.
- Maule, A.G. and H.F. Horton. 1985. Probable couses of the rapid growth and high fecundity of walleye, *Stizostedion vitreum vitreum*, in the mid-Columbia River. Fishery Bulletin 83: 701-706.
- Mesa, M. M., T. P. Poe, D. M. Gadomski, and J. H. Petersen. 1994. Are all prey created equal? A review and synthesis of differential predation on prey of substandard condition. Journal of Fish Biology 45: 81-96.
- Mesa, M.M., L.K. Weiland, and P. Wagner. 2002. Effects of acute thermal stress on the survival, predator avoidance, and physiology of juvenile fall Chinook salmon. Northwest Science 76: 118-128.
- Miglavs, I., and M. Jobling. 1989. Effects of feeding regimes on food consumption, growth rates and tissue nucleic acids in juvenile Arctic charr <u>Salvelinus alpinus</u>, with particular respect to compensatory growth. Journal of Fish Biology 34:947-957.

- Miller, D.R.. 1993. Columbia River American Shad—An Overview. National Marine Fisheries Service, Seattle, WA. March, 1993.
- Monk, B., D. Weaver, C. Thompson, and F. Ossiander. 1989. Effects of flow and weir design on the passage behavior of American shad and salmonids in an experimental fish ladder. North American Journal of Fisheries Management 9: 60-67.
- Muir, W.D., S.G. Smith, K.W. McIntyre, and B.P. Sandford. 1998. Project survival of juvenile salmonids passing through the bypass system, turbines, and spillways with and without flow deflectors at Little Goose Dam, 1997. Annual report to the U.S. Army Corps of Engineers, Walla Walla, Washington, contract E86970085, 47 p.
- Olney, F.E.. 1974. Life history and ecology of the northern squawfish <u>Ptychocheilus oregonensis</u> (Richardson) in Lake Washington. M.S. Thesis, University of Washington, Seattle. 73 p.
- Parker, R.M., M.P. Zimmerman, and D.L. Ward. 1995. Variability in the biological characteristics of northern squawfish in the lower Columbia and Snake rivers. Transactions of the American Fisheries Society 124: 335-346.
- Perry, R. W., S.D. Fielding, A.D. Cochran, J.L. Schei, J.M. Sprando, G.T. George, N.S. Adams, and D.W. Rondorf. 2003. Turbine survival and migration behavior of subyearling Chinook salmon at McNary Dam, 2003. Bonneville Power Administration, Draft report of research, Contract 00014243, November 2003.
- Petersen, J. H.. 1994. The importance of spatial pattern in estimating predation on juvenile salmonids in the Columbia River. Transactions of the American Fisheries Society 123: 924-930.
- Petersen, J.H., D.B. Jepsen, R.D. Nelle, R.S. Shively, R.A. Tabor, and T.P. Poe. 1990. System-wide significance of predation on juvenile salmonids in Columbia and Snake River reservoirs. Annual report to Bonneville Power Administration 1990, contract DE-AI79-90BP07096. Portland, OR.
- Petersen, J.H., S.T. Sauter, C.N. Frost, S.R. Gray, and T.P. Poe. 1992. Indexing juvenile salmonid consumption by northern squawfish in the Columbia River below Bonneville Dam and in John Day Reservoir, 1992. *In*: J.H. Petersen and T.P. Poe (eds.) System-wide significance of predation on juvenile salmonids in Columbia and Snake river reservoirs. Annual report to Bonneville Power Administration 1992, contract DE-AI79-90BP07096. Portland, OR.
- Petersen, J. H., and D. L. DeAngelis. 1992. Functional response and capture timing in an individual-based model: predation by northern squawfish (*Ptychocheilus oregonensis*) on juvenile salmonids in the Columbia River. Canadian Journal of Fisheries and Aquatic Science 49: 2551-2565.
- Petersen, J.H. and D. L. Ward. 1999. Development and corroboration of a bioenergetics model for northern squawfish feeding on juvenile salmonids in the Columbia River. Transactions of the American Fisheries Society 128: 784-801.
- Petersen, J.H., C.A. Barfoot, S.T. Sauter, D.M. Gadomski, P.J. Connolly, and T.P. Poe. 2000. Predicting the effects of dam breaching in the lower Snake River on losses of juvenile salmonids to predators. Report to Army Corp of Engineers, Walla Walla District, Walla Walla, WA.
- Petersen, J.H., R.A. Hinrichsen, D.M. Gadomski, D.H. Feil, and D.W. Rondorf. 2003. American shad in the Columbia River.
- Petersen, J. H.. Report A, In preparation. Variation in growth rates of northern pikeminnow in the lower Columbia and Snake rivers.
- Peters, J.C.. 1964. Summary of calculated growth data on Montana fishes, 1948-61. Montana Fish and Game Department. D-J Job Completion Report F-23-A-6. 76 p.
- Pflug, D.E. and G.B. Pauley. 1984. Biology of smallmouth bass (*Micropterus dolomieui*) in Lake Sammamish, Washington. Northwest Science 58:118-130.
- Poe, T.P., H.C. Hansel, S.Vigg, D.E. Palmer, and L.A. Preendergast. 1988. Predation by northern squawfish, walleye, smallmouth bass, and channel catfish in a mainstem Columbia river reservoir: I. Feeding ecology during the salmonid smolt out-migration, p. 13-55. *In*: T.P. Poe

- (ed.) Predation by resident fish on juvenile salmonids in John Day Reservoir. Vol. I. Final report of research to Bonneville Power Administration. U.S. Fish and wildlife Service, National Fishery Research Center, Cook, WA.
- Poe T. P., H. C. Hansel, S. Vigg, D. E. Palmer, and L. A. Prendergast. 1991. Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:405-420.
- Poe, T. P., R. S. Shively, and R. A. Tabor. 1994. Ecological consequences of introduced piscivorous fishes in the lower Columbia and Snake rivers. *In*: D. J. Stouder, K. L. Fresh, and R. J. Feller, editors, Theory and Application in Fish Feeding Ecology. University of South Carolina Press, Columbia, South Carolina, USA.
- Quinn, T.P., and Adams, D.J.. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. Ecology 77:1151 1162.
- Quinn, T.P., S. Hodgson, and C. Peven. 1997. Temperature, flow, and the migration of adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. Canadian Journal of Fish and Aquatic Sciences 54:1349-1360.
- Rahrer, J.F.. 1963. Age and growth of four species of fish from Flathead Lake, Montana. Proc. Montana Acad. Sci. 23:144-156.
- Rawson, D.S.. 1957. The life history and feeding ecology of the yellow walleye, <u>Stizostedion vitreum</u>, in Lac la Ronge, Saskatchewan. Transactions of the American Fisheries Society 86:15-37.
- Reid, G.E. 1971. Life history of the northern squawfish <u>Ptychocheilus oregonensis</u> (Richardson) in the St. Joe River, Idaho. M.S. Thesis, University of Idaho, Moscow. 61 p.
- Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120:448-458.
- Roby, D.D., D.P. Craig, K. Collis, and S.L. Adamany. 1998. Avian predation on juvenile salmonids in the lower Columbia River. U.S. Army Corps of Engineers, Portland, Oregon.
- Roell, M.J. and D.J. Orth. 1993. Trophic basis of production of stream-dwelling smallmouth bass, rock bass, and flathead catfish in relation to invertebrate bait harvest. Transactions of the American Fisheries Society 122:46-62.
- Roell, M. J., and D. J. Orth. 1998. Indirect effects of fishery exploitation and pest control in a riverine food web. North American Journal of Fisheries Management 18:337-346.
- Rondorf, D. W., M. S. Dutchuk, A. S. Kolok, and M. L. Gross. 1985. Bioenergetics of juvenile salmon during the spring outmigration. Bonneville Power Administration, Portland, Oregon.
- Rottiers, D. V., and R. M. Tucker. 1982. Proximate composition and caloric content of eight Lake Michigan fishes. U.S. Fish and Wildlife Service Technical Papers 108:1-8.
- Sammons, S.M. and P.W. Bettoli. 1999. Spatial and temporal variation in electrofishing catch rates of three species of Black Bass (*Micropterus* spp.) from Normandy Reservoir, Tennessee. North American Journal of Fisheries Management 19: 454 461.
- Sauter, S.T. and J.H. Petersen. Report B, in preparation. The role of American shad in the fall diet of northern pikeminnow.
- Sauter, S.T. and J.H. Petersen. Report C, in preparation. Bioenergetics modeling on northern pikeminnow.
- Sauter, S.T. and J.H. Petersen. Report D, in preparation. Historical changes in piscivory on juvenile salmonids in the lower Columbia River.
- Sechnick, C.W., R.F. Carline, R.A. Stein, and E.T. Ranken. 1986. Habitat selection by smallmouth bass in response to physical characteristics of a simulated stream. Transactions of the American Fisheries Society 115: 314-321.

- Serns, S.L.. 1984. Walleye growth in relation to water temperature, food availability, and population density in Escanaba Lake, 1956-82. Wisconsin Department of Natural Resources, Research Report 130, Madison.
- Shively, R.S., R.A. Tabor, R.D. Nelle, D.B. Jepsen, J.H. Petersen, S.T. Sauter, and T.P. Poe. 1991. System-wide significance of predation on juvenile salmonids in the Columbia and Snake river reservoirs. Annual report of research to Bonneville Power Administration, contract DE-AI79-90BP07096.
- Shively, R. S., T. P. Poe, and S. T. Sauter. 1996. Feeding response by northern squawfish to a hatchery release of juvenile salmonids in the Clearwater River, Idaho. Transactions of the American Fisheries Society 125:230-236.
- Shrimpton, J.M., J.D. Zydlewski, and S.D. McCormick. 2001. The stress response of juvenile American shad to handling and confinement is greater during migration in freshwater than in seawater. Transactions of the American Fisheries Society 130:1203-1210.
- Sims, C.W., W.W. Bentley, and R.C. Johnsen. 1977. Effects of power peaking operations on juvenile salmon and steelhead trout migrations—progress 1976. Report to the U.S. Army Corps of Engineers. National Marine Fisheries Service, Northwest Fisheries Center, Seattle, Washington, USA.
- Sims, C.W., W.W. Bentley, and R.C. Johnsen. 1978. Effects of power peaking operations on juvenile salmon and steelhead trout migrations—progress 1977. Report to the U.S. Army Corps of Engineers. National Marine Fisheries Service, Northwest Fisheries Center, Seattle, Washington, USA.
- Smith, S.G., W.D. Muir, E.E. Hockersmith, R.W. Zabel, R.J. Graves, C.V. Ross, W.P. Connor, B.D. Arnsberg. 2003. Influence of river conditions on survival and travel time of Snake River subyearling fall Chinook salmon. North American Journal of Fisheries Management 23: 939-961.
- Stewart, D. J., D. Weininger, D.V. Rottiers, and T.A. Edsall. 1983. An energetics model for lake trout, <u>Salvelinus namaycush</u>: appliecation to the Lake Michigan population. Canadian Journal of Fisheries and Aquatic Sciences. 40:681-698.
- Stroud, R.H.. 1949. Growth of Norris Reservoir walleye during the first twelve years of impoundment. Journal of Wildlife Management 13:157-177.
- Tabor, R. A., R. S. Shively, and T. P. Poe. 1993. Predation on juvenile salmonids by smallmouth bass and northern squawfish in the Columbia River near Richland, Washington. North American Journal of Fisheries Management 13: 831-838.
- Tiffan, K.F., C.A. Haskell, and D.W. Rondorf. 2003. Thermal exposure of juvenile fall Chinook salmon migrating through a lower Snake River reservoir. Northwest Science 77: 100-209.
- Tinus, E.S. and R.C. Beamesderfer. 1994. An update on the distribution, fisheries, and biology of walleye in the lower Columbia River. Oregon Dept. of Fish and Wildlife Information Report 94-3.
- Todd, B.L. and C.F. Rabeni. 1989. Movement and habitat use by stream-dwelling smallmouth bass. Transactions of the American Fisheries Society 118: 229-242.
- Tyler, A.V., and R.S. Dunn. 1976. Ration, growth, and measures of somatic and organ conditions in relation to meal frequency in winter flounder, <u>Pseudopleuronectes americanus</u>, with hypotheses regarding population homeostasis. Journal of the Fisheries Research Board of Canada 33:63-75.
- Vigg, S. and C.C. Burley. 1991. Temperature-dependent maximum daily consumption of juvenile salmonids by northern squawfish (*Ptychocheilus oregonensis*) from the Columbia River. Canadian Journal of Fish and Aquatic Sciences 48: 2491-2498.
- Vigg, S., T. P. Poe, L. A. Prendergast, and H. C. Hansel. 1991. Rates of consumption of juveniles salmonids and alternative prey fish by northern squawfish, walleyes, smallmouth bass, and

- channel catfish in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 120: 421-438.
- Ward, D. L., J. H. Petersen, J. J. Loch. 1995. Index of predation on juvenile salmonids by northern squawfish in the lower and middle Columbia River and in the lower Snake River. Transactions of the American Fisheries Society 124: 321-334.
- Ware, D.M. 1972. Predation by rainbow trout <u>Salmo gairdneri</u>: the influence of hunger, prey density, and prey size. Journal of the Fisheries Research Board of Canada 29:1193-1201.
- Warner, K. 1972. Further studies of fish predation of salmon stocked in Maine lakes. Progressive Fish-Culturist 34:217-221.
- Yearsley, J.. 1999. Columbia River temperature assessment: simulation methods. U.S. Environmental Protection Agency, Region 10, Seattle, Washington. 74 p. plus Appendices.
- Zimmerman, M.P. and R.M. Parker. 1995. Relative density and distribution of smallmouth bass, channel catfish, and walleye in the lower Columbia and Snake Rivers. Northwest Science 69: 19-28.
- Zimmerman, M.P. 1999. Food habits of smallmouth bass, walleyes, and northern pikeminnow in the lower Columbia River basin during outmigration of juvenile anadromous salmonids. Transactions of the American Fisheries Society 128: 1036-1054.

# Appendix A

## A Brief History of the Smolt Condition Project (1987 – 2003)

The Assessment of Smolt Condition for Travel Time Analysis Project (Bonneville Power Administration Project 87-401; ASCTTA) monitored attributes of wild and hatchery salmonid smolt physiology in the Columbia River Basin from 1987 to 1997 under the Northwest Power Planning Council Fish and Wildlife Program, in cooperation with the Smolt Monitoring Program of the Fish Passage Center (Table 1). The primary goal of the project was to investigate the physiological development of juvenile salmonids related to migration rates. The assumption was made that the level of smolt development, interacting with environmental factors such as flow, would be reflected in travel times. The Fish Passage Center applied the physiological measurements of smolt condition to Water Budget management, to regulate flows so as to decrease travel time and increase survival.

Significant findings were that in-river migration played an important role in the development of smoltification, as measured by gill sodium, potassium ATPase levels and condition factor. A characteristic profile of low ATPase activities in the hatchery with increasing ATPase activities during the migration was found for Columbia basin salmonid stocks. Differences in predictors of travel times were found between chinook salmon and steelhead. Riverflow was the only significant predictor of travel time in steelhead, while river flow and changes in flow, ATPase activity, condition factor, and water temperature are significant predictors in spring chinook salmon. Bacterial kidney disease prevalence in juvenile migrants was evaluated and differences in prevalence and changes during the migration were found between the Columbia and Snake rivers. Prevalence of the pathogen in Snake River fish that were exposed to higher water temperatures and longer migration distances, increased after release.

Other indices of smolt condition that correlate with gill ATPase activity were developed by the project: a morphometric index describing changes in body shape, a skin reflectance method that quantifies silvering and guanine deposition, and a microassay for gill ATPase. Technical assistance was provided to regional fishery agencies on cooperative projects to evaluate the physiological effects of adaptive management strategies, including modified hatchery rearing protocols, natural rearing methods, and release and acclimation programs.

In 1995 the fisheries management agencies began a voluntary spill program to insure that a high proportion of emigrating salmonids passed dams via routes other than turbines. As a result, concerns arose about the impact of gas supersaturated water on smolt survival. In response to regional requests, ASCTTA developed a non-lethal method to detect gas bubble disease (GBT) in juvenile salmonids. In 1996, Gas Bubble Disease Research and Monitoring of Juvenile Salmonids (BPA Project 1996-02100) spun off from the ASCTTA to address critical uncertainties associated with GBT (Table 1).

In 1997, as the focus of the project began changing, we summarized the first 10-years of the project (Table 2), and developed and distributed a hatchery survey to evaluate how rearing conditions at ASCTTA reference hatcheries may have influenced annual changes in smoltification. In 1998 data collected from the hatcheries were combined with our physiological data to determine which rearing factors make the greatest contribution to juvenile migration

success. These data were combined in to a geographic information system titled "Biologically Intergrated Geospatial Salmonid data Access Management: BIGSAM". BIGSAM became available on a CD in 2001 and has been widely distributed.

To reflect the changing nature of the research conducted by the project, in 1999 the name was changed to *Assessment of Smolt Condition: Biological and Environmental Interactions*. Since then, the project's main focus has been to work with other research projects in the region to determine the impact of hatchery practices on post-release survival. Although the Smolt Project ended in March 2004, we continue to work with the US Fish & Wildlife Service and the University of Idaho to assess the impact of water source on immune system development and survival of juvenile spring Chinook salmon (Table 1).

There have been 15 peer-reviewed publications, 12 project reports and one GIS published during the course of this project (Table 1 & 2; Project Publications).

Table 1. Dates of major activities for *Assessment of Smolt Condition* (BPA project 19870400) from 1987 to 2004.

Dates	Major Activities		
1987-1996	Assessment of smolt condition for travel time analysis for in-season use by the Water Budget.		
1995 –1996	Non-lethal assessment of gas bubble disease; project spin-off.		
1997	10-year report of Smolt Assessment Project.		
	$\underline{http://www.efw.bpa.gov/Environment/EW/EWP/DOCS/REPORTS/DOWNSTRM/D35245-7.pdf}$		
1997-1998	Query hatcheries for practices that might influence migration and survival of juvenile salmonids.		
2000-2002	Biologically Integrated Geospatial Salmonid data Access Management: BIGSAM. CD is available.		
1999-2005	Hatchery versus wild studies to determine the impacts of water source on development and survival		

DOE ID	Rpt Years	PubDate	Title; SubTitle
<u>35245-2</u>	1988-1988	03/89	Assessment of Smolt Condition for Travel Time Analysis;
<u>35245-3</u>	1989-1989	11/90	Assessment of Smolt Condition for Travel Time Analysis;
<u>35245-4</u>	1990-1990	12/91	Assessment of Smolt Condition for Travel Time Analysis;
<u>35245-5</u>	1991-1992	05/94	Assessment of Smolt Condition for Travel Time Analysis;
<u>35245-7</u>	1987-1997	12/97	Assessment of Smolt Condition for Travel Time Analysis;
<u>35245-8</u>	1993-1994	02/99	Assessment of Smolt Condition for Travel Time Analysis;
<b>35245-10</b>	1990-1996	04/00	Assessment of Smolt Condition for Travel Time Analysis;

Table 2. Summary of additional project reports available on the BPA website.

### **Project Publications**

- Beeman, J. W., and D. W. Rondorf. 1992. Effects of flow and smoltification on the migration rates of spring chinook salmon and steelhead. Pages 77-83. In Proceedings of the Atlantic Salmon Workshop, U.S. Fish and Wildlife Service, Lamar, Pennsylvania.
- Beeman, J. W., D. W. Rondorf, J. C. Faler, M. E. Free, P. V. Haner, S. T. Sauter, and D. A. Venditti. 1991. Assessment of smolt condition for travel time analysis. Annual Report 1990 (Contract DE-A179-87BP35245) to Bonneville Power Administration, Portland, Oregon.
- Beeman, J. W., D. W. Rondorf, and M. E. Tilson. 1994. Assessing smoltification of juvenile spring chinook salmon (*Oncorhynchus tshawytscha*) using changes in body morphology. Canadian Journal of Aquatic and Fisheries Sciences 51: 836-844.
- Beeman, J. W., D. W. Rondorf, M. E. Tilson, and D. A. Venditti. 1995. A non-lethal measure of smolt status of juvenile steelhead based on body morphology. Transactions of the American Fisheries Society 124: 764-769.
- Gannam, A.L. and R.M. Schrock, 1999. Immunostimulants in fish diets. Journal of Applied Aquaculture 9: 53-70.

- Gannam, A.L. and R.M. Schrock, 2001. Immunostimulants in fish diets. In: Lim, C. and C.D. Webster (eds), Nutrition and fish health, Food Products Press, Binghamton, New York, USA.
- Haner, P. V., J. C. Faler, R. M. Schrock, D. W. Rondorf, and A. G. Maule. 1995. Skin reflectance as a non-lethal measure of smoltification for juvenile salmonids. North American Journal of Fisheries Management 15: 814-822.
- Maule, A.G. and M.G. Mesa, 1994. Efficacy of electrofishing to assess plasma cortisol concentration in juvenile Chinook salmon passing hydroelectric dams on the Columbia River. North American Journal Fisheries Management 14: 334-339.
- Maule, A. G., J. W. Beeman, R. M. Schrock, and P. V. Haner. 1994. Assessment of smolt condition for travel time analysis. Annual Report 1991-1992 (Contract DE-A179-87BP35245) to Bonneville Power Administration, Portland, Oregon.
- Maule, A. G., D. W. Rondorf, J. W. Beeman, and P. V. Haner. 1996. Epizootiology of *Renibacterium salmoninarum* in juvenile hatchery spring chinook salmon in the Columbia and Snake rivers. Journal of Aquatic Animal Health 8: 37-46.
- Maule, A. G., R. M. Schrock, C. Slater, M. S. Fitzpatrick, and C. B. Schreck. 1996. Immune and endocrine responses of adult spring chinook salmon during freshwater migration and sexual maturation. Fish and Shellfish Immunology 6: 221-233.
- Rondorf, D. W., J. W. Beeman, J. C. Faler, M. E. Free, and P. V. Haner. 1990. Assessment of smolt condition for travel time analysis. Annual Report 1989 (Contract No. DE-A179-87BP35245) to Bonneville Power Administration, Portland, Oregon.
- Rondorf, D. W., J. W. Beeman, J. C. Faler, M. E. Free, and E. J. Wagner. 1989. Assessment of smolt condition for travel time analysis. Annual Report 1988 (Contract No. DE-A179-87BP35245) to Bonneville Power Administration, Portland, Oregon.
- Rondorf, D. W., J. W. Beeman, M. E. Free, and D. E. Liljegren. 1988. Correlation of biological characteristics of smolts with survival and travel time. Annual report 1987 (Contract DE-A179-87BP35245) to Bonneville Power Administration, Portland, Oregon.
- Sauter, S.T., L.I. Crawshaw, and A.G. Maule, 2001. Behavioural thermoregulation by juvenile spring and fall Chinook salmon, *Oncorhynchus tshawytscha*, during smoltification. Environ. Biol. Fish. 61: 295-304.
- Schrock, R. M., J. W. Beeman, D. W. Rondorf, and P. V. Haner. 1994. A microassay for gill sodium, potassium-activated ATPase in juvenile Pacific salmonids. Transactions of the American Fisheries Society 123: 223-229.

- Schrock, R.M., S.D. Smith, A.G. Maule, S.K. Doulos, and J.J. Rockowski, 2001. Mucous lysozyme levels in hatchery coho salmon (*Oncorhynchus kisutch*) and spring Chinook salmon (*O. tshawytscha*) early in the parr-smolt transformation. Aquaculture 198: 169-177.
- VanderKooi, S.P., W.L. Gale, and A.G. Maule, 2000. Preliminary study of gill Na<sup>+</sup>,K<sup>+</sup>-ATPase activity in juvenile spring Chinook salmon following electroshock or handling stress. N. Am. J. Fish. Manage. 20: 528-533.
- VanderKooi, S.P. and A.G. Maule, 1999. Prevalence of *Renibacterium salmoninarum* in juvenile spring Chinook salmon at Columbia and Snake River hatcheries, 1993-1996. J. Aquat. Anim. Health 162-169.
- VanderKooi, S.P., A.G. Maule, and C.B. Schreck, 2001. The effects of electroshock on immune function and disease progression in juvenile spring Chinook salmon. Trans. Am. Fish. Soc. 130: 397-408.